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New species of fossil Neritidae, Neridomidae, and Otostomidae (Gastropoda: Neritoidea) from Texas, Tennessee, and Alabama

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ABSTRACT

Nine new species of neritoidean gastropods are described from the fossil record of the Gulf Coastal Plain of the United States, eight of which are named and one is left in open nomenclature. *Otostoma cattoi* new species, *Otostoma* sp., and *Neridomus mccallae* new species, are from the Cretaceous (Albian) Edwards Formation of Texas. *Neridomus minutissimus* new species is from the Cretaceous (Albian) Walnut Formation of Texas. The genus *Neridomus* has not thus far been reported from the Cretaceous of the USA. *Clithon cooncreekense* new species is from the Cretaceous (Maastrichtian) Coon Creek type locality in Tennessee and is the first neritid reported from that site. *Pseudodostia lisbonensis* new species is from the Eocene (Bartonian) Lisbon Formation of Alabama. From the Eocene (Lutetian) Cook Mountain Formation of Texas, *Clithon duomillias* new species is from the Landrum Member, *Clithon lisae* new species is from the Wheelock Member, and *Clithon traceyi* new species is from the Stone City Member. These are the first reported neritids from the Eocene (Claibornian Stage) of the Gulf Coastal Plain.

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Additional Keywords: Marine, freshwater, fossil, Cretaceous, Eocene

INTRODUCTION

The family Neritidae is known from the Triassic (Tracey et al., 1993) to the Present. Recent Neritidae are intertidal on rocky shores (*Nerita* Linnaeus, 1758) or live in freshwater (*Theodoxus* Montfort, 1810) or in brackish water (*Clithon* Montfort, 1810, *Neritina* Lamarck, 1816, various genera previously regarded as subgenera of *Neritina*, such as *Vitta* Mörch, 1852 and *Vittina* Baker, 1923, and a few *Nerita*). Both *Clithon* and *Neritina* live as adults in fresh or brackish water but have a marine planktotrophic larval stage, the veligers being washed downstream and out to sea where they live in the plankton, swimming with the aid of a quadrilobed velum and feeding on algal cells. The exact duration of this stage is unknown, but is likely to be a minimum of several weeks and may well vary between species (Bandel, 2001: 73–76). During this period, the larval shell is formed, following which they settle in river mouths and crawl upstream, many species eventually reaching freshwater (Bandel, 2001: 97). Neritidae often live at considerable densities and form an important part of the molluscan fauna. *Clithon oualaniense* (Lesson, 1831), as an example, is abundant in suitable locations in mangroves in Vietnam (Zvonareva et al., 2015, table 2). It is apparent from the deposits in which they are found that fossil Neritidae occupied similar habitats to Recent genera and in suitable brackish horizons they can be very common. For instance, the "Neritina Bed" in the Colwell Bay Member of the Headon Hill Formation, Solent Group, late Eocene (Insole and Daley 1985) contains abundant *Clithon concavum* (J. de C. Sowerby, 1823) at Colwell Bay and at Headon Hill in the Isle of Wight, England (Symonds, 2006: 33). In wholly marine offshore sediments, they are non-existent or very rare, only occurring as a result of having been swept downstream and out to sea, perhaps during storm events. Neritidae are generally rare in the Eocene of the U.S., only four to date from the Eocene of the Gulf Coastal Plain, *Neritina unidentata* Aldrich, 1911 from the early Eocene Hatchetigbee Formation of Alabama, *Theodoxus domicilium* Garvie, 1996, from the middle Eocene Reklaw Formation of Texas, *Velates floridanus* Richards, 1946, from the late Eocene, Inglis Formation of Florida, and *Pseudodostia ocalana* Vermeij and Portell, 2013, from the late Eocene Ocala Limestone of Florida. Many more have been described from the Eocene of the Pacific Coast (Groves and Squires, 2021). The species described herein, with the exception of *C. traceyi* new species, are all known from only from a single specimen, indicating that they were living at some distance from the localities at which they were found, and were transported there by ocean currents.

Neridomidae and Otostomidae are extinct families and consequently their habitats can only be deduced from the deposits in which they are found. According to Bandel (2008: 28), *Neridomus* inhabited shallow marine environments, probably estuaries. *Otostoma* are particularly

common in Late Cretaceous marine sediments which are indicative of shallow, subtropical, warm-water conditions (Saul and Squires, 1997: 138).

MATERIALS AND METHODS

The Lower Cretaceous material is from three localities in the Albian stage, in central Texas and is catalogued within the Non-vertebrate Paleontology Laboratory, Jackson School of Geosciences, The University of Texas at Austin (NVP) collections. Two of the above localities are in the Edwards Formation and both were temporary exposures; the first was a road construction site in Georgetown, Texas, which turned out to have the largest and most diverse assemblage of Edwards Formation fossils ever found at a single locality (McCall et al., 2008); at this site, aragonitic fossils were preserved as calcitic pseudomorphs. The second locality was a temporary exposure within the town of Round Rock, Texas, exposed during housing construction; at this site, the fossils are preserved as silicified pseudomorphs. The third locality exposes the Walnut Formation along Rt. 107, Coryell County, Texas, and this site has furnished a diverse fauna of small to minute species, which suggests a shallow-water near-shore environment. The Edwards Formation is the uppermost formation in the Lower Cretaceous Albian stage and extends over a wide area from central Texas to the Pecos Valley area in west Texas and over most of this area is a cherty, dolomitic, rudist-bearing limestone (Lozo et al., 1959).

The Eocene and Upper Cretaceous material was collected by the senior author and was originally part of his personal collection. The Upper Cretaceous specimen was found at the classic Coon Creek Formation type locality in McNairy County, Tennessee (Wade, 1926). In Wade (1926), the formation at the Coon Creek type locality is designated as the Ripley Formation. The updated stratigraphy here follows Russell and Parks (1975), and Wingard (1993). The Eocene specimens were all collected from strata of the Claiborne Group. The Alabama specimen was collected from a glauconitic, calcareous, clayey sand lens in the Lisbon Formation at Little Stave Creek (Gardner, 1957), just downstream from the base of the Gosport Sand Formation and equivalent to the Cook Mountain Formation of Texas. The Cook Mountain Formation is subdivided into four members, in order of decreasing age: Stone City Member, Wheelock Member, Landrum Member, and Mount Tabor Member. For inferred synopsis of the environmental conditions of the above members see Garvie et al. (2020: 9–10). Specimens were collected from localities in each of the three lowest members. The Cook Mountain Formation is primarily a unit of mudstones and interbedded sandstones sometimes with glauconitic sandstones, black shale beds, and siderite-cemented beds (Barnes, 1982). All specimens, for each locality, were collected from sand lenses within the mudstones and probably represented wave or current dominated accumulations so specimens were likely transported from other locations.

The junior author was responsible for the systematics of the taxa. All specimens were photographed with a 12 Mp Canon camera. Focal stacking layering (multiple images) was used on all specimens, Adobe Photoshop CC was used to ready the images for publication.

Repository and institutional acronym: All specimens are deposited in the Non-vertebrate Paleontology Laboratory, Jackson School of Geosciences, The University of Texas at Austin (NVP).

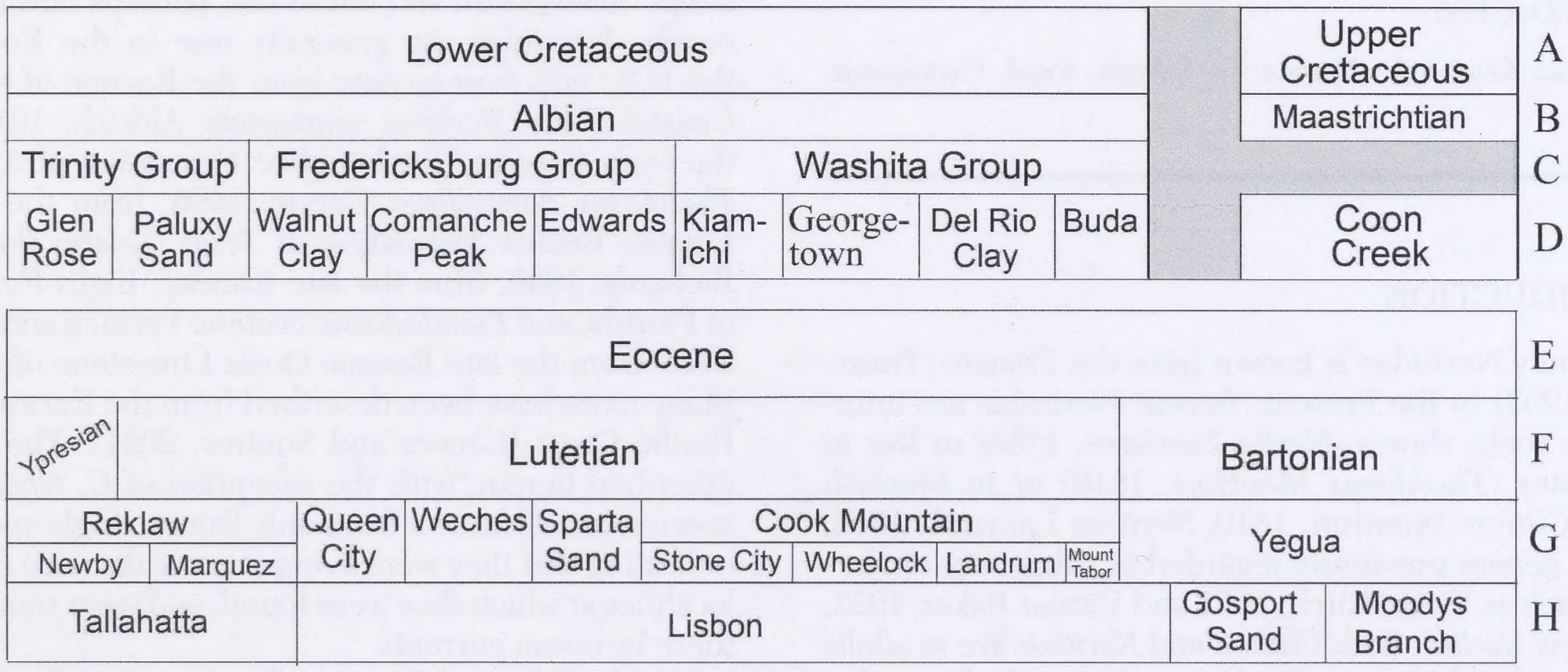


Figure 1. Stratigraphic chart indicating the relative positioning of the individual units within the Cretaceous system and Eocene epoch where the specimens were found. **A.** Cretaceous Series. **B.** Cretaceous Stages. **C.** Groups within the Albian of Texas. **D.** Formations within the Albian of central Texas and the Maastrichtian of Tennessee. **E.** Epoch. **F.** Eocene Stages. **G.** Formation and members within the middle Eocene in central Texas. H. Formations within the middle Eocene of Alabama.

SYSTEMATICS

Superorder Neritimorpha Golikov and Starobogatov, 1975
Order Cycloneritimorpha Bandel and Frýda, 1999
Superfamily Neritoidea Rafinesque, 1815
Family Neridomidae Bandel, 2008

Genus *Neridomus* Morris and Lycett, 1851

Type Species: *Neridomus anglicus* Cox and Arkell, 1950, fixed as type species under Article 70.3 of the International Code of Zoological Nomenclature (Bouchet et al. 2017: 162). Jurassic, England.

Description: Shell smooth, ovately globose; spire small, oblique; the last whorl very large; aperture ovate, or semilunar; outer lip thick; inner lip thick, convex and smooth. (Morris and Lycett 1851: 57).

Remarks: Wenz (1938: 415) considered *Neridomus* to be a subgenus of *Neritoma* Morris, 1849 and he was followed by subsequent authors including Keen (1960: I280), Allison (1955: 413) and Kase (1984: 86). However, *Neritoma* has a distinctive sinus in the outer lip, a feature that is entirely lacking in *Neridomus*. Bandel (2008: 28) restored *Neridomus* to generic level. *Neritodomus* Fischer, 1885 is now considered to be an unjustified emendation of *Neridomus*.

***Neridomus mccallae* new species**
(Figures 7–8)

Diagnosis: Small *Neridomus*; protoconch exserted; teleoconch about two rapidly expanding whorls, last comprising most of shell; spire low. Aperture wide, semi-elliptic; outer lip forming narrow gutter adapically at junction with septum.

Description: Small *Neridomus*; protoconch worn on only known specimens, exserted; teleoconch hemispherical, about two rapidly expanding, evenly rounded whorls, the last comprising most of the shell, surface smooth; spire low, suture narrow. Aperture wide, semi-elliptic; outer lip thin, smooth within, forming long, narrow gutter adapically where it joins the septum; septum broad, smooth, convex, sloping into aperture at approximately 38°, adapical edge of callus sinuous; septum edge straight, rounded, edentate, with small concavity at adapical end.

Type Locality: Temporary roadcut exposure in 2011 during construction of Interstate Highway10, on the east side of the road, just south of the bridge over the south fork of the San Gabriel River, Georgetown, Williamson County, Texas, USA. GPS: 30°37′28.62″ N, 97°41′30.15″ W.

Type Material: Holotype: NPL95470 (Figures 2–4), paratype: NPL54091, Lower Cretaceous, Albian, Fredericksburg Group, Edwards Formation.

Dimensions: Holotype: NPL95470, height 7 mm, width 7.8 mm, paratype: NPL54091, height 6.2 mm, width 6.8mm.

Etymology: Named in honour of Linda McCall who discovered the fossiliferous section at this location and collected much material from the site.

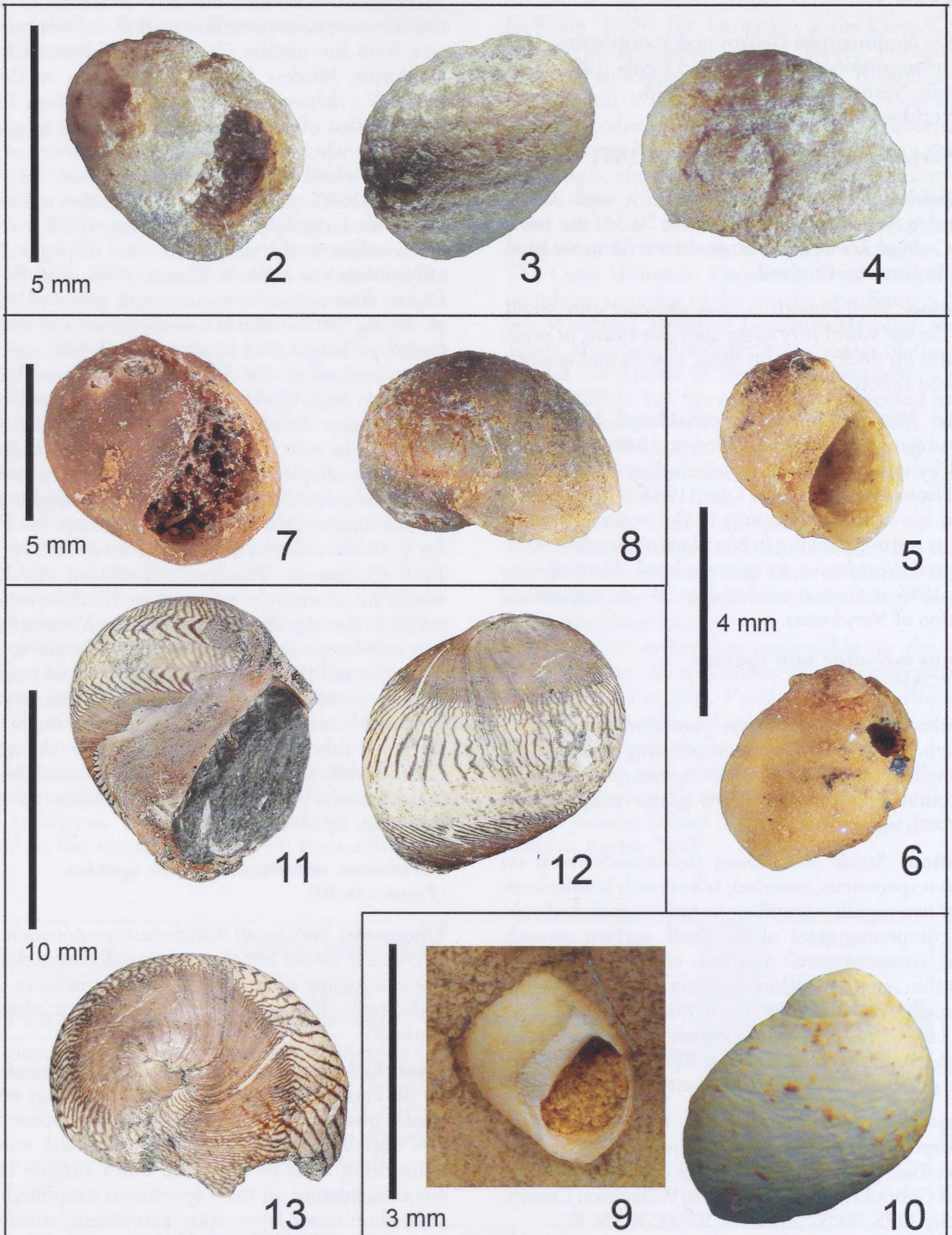
Remarks: *Neridomus mccallae* is similar to *Neritoma* (*Neridomus*) *delpeyae* Allison, 1955, an even smaller species from the middle Cretaceous of Punta China, Baja California, Mexico. However, the callus on the septum of *N.* (*N.*) *delpeyae* is parallel-sided (Allison 1955: 413) whereas that of *N. mccallae* has a sinuous adapical edge. The body whorl of *N. mccallae* covers more of the penultimate whorl than is the case with *N.* (*N.*) *delpeyae* (Allison 1955, pl. 40, fig. 10), and the narrow gutter where the outer lip joins the septum, which is a feature of *N. mccallae*, is absent from *N.* (*N.*) *delpeyae*. *Neritoma* (*Neridomus*) *woodfordi* Allison, 1955, also from Punta China, does appear to have a small gutter (Allison 1955, pl. 40, fig. 16) but that is a much larger and heavier shell (holotype height 21.7 mm) with a slightly concave posterior surface on the body whorl (Allison 1955: 413), while the body whorl on *N. mccallae* is evenly rounded. *Neritodomus dolichostoma* Cossmann, 1907 from the Early Cretaceous, Barremian of Languedoc-Roussillon, France is another species similar to *N. mccallae* but, again, substantially larger; 20 mm in height according to Cossmann (1907: 24). Kase (1984, pp. 86–87, pl. 10, fig. 9, 10) described a *Neritoma* (*Neridomus*) sp. from the Early Cretaceous, Hiraiga Formation of Miyako, Japan, which he tentatively referred to *N. dolichostoma* and which is also significantly larger than *N. mccallae* (of the two specimens figured by Kase, the larger is 19.8 mm in height and the smaller 19.2 mm). Apart from the difference in size, the spire on *N. dolichostoma* is scarcely protruded, according to Kase, whereas on *N. mccallae* the spire although low, is clearly visible; the aperture is narrow, while that of *N. mccallae* is wide and the outer lip is moderately thick and slightly bevelled in contrast to the thin outer lip of *N. mccallae*.

***Neridomus minutissimus* new species**
(Figures 9–10)

Diagnosis: Very small *Neridomus*: protoconch exserted; teleoconch rather less than two rapidly expanding whorls, last comprising most of shell; spire prominent. Aperture wide, semi-elliptic; septum callus narrow, adapical edge sinuous.

Description: Very small *Neridomus*; protoconch worn on all known specimens, exserted, junction with teleoconch obscured; teleoconch probably rather less than two rapidly expanding, evenly rounded whorls, last comprising most of the shell, outer surface layer thin, smooth, missing on most specimens examined exposing crystalline inner layer; spire prominent, suture narrow. Aperture wide, semi-elliptic; outer lip thin, smooth within; short gutter at adapical junction with septum; septum narrow, smooth, convex, adapical edge of callus sinuous; septum edge straight or slightly concave, rounded, edentate.

Type Locality: Thin silicified layer at top of roadcut on Highway 107, 1.44 km west of junction with Highway 1829, Coryell County. Texas. GPS: 31°23′7.48″ N, 97°38′9.97″ W.



Figures 2–13. New species of fossil Otostomidae, Neridomidae, and Neritidae. **2–4. *Otostoma cattoi* new species,** holotype NPL96587. Apical, lateral, and apertural views. Albian, Edwards Formation. **5–6**. ***Otostoma* sp**. figured specimen NPL54112. Apertural and lateral views. Albian, Edwards Formation. **7–8. *Neridomus mccallae* new species,** holotype NPL95470. Apertural and apical views. Albian, Edwards Formation. **9–10. *Neridomus minutissimus* new species,** holotype NPL95468, apertural view; paratype NPL95469, rear view. Albian, Walnut Formation. **11–13. *Clithon cooncreekense* new species,** holotype NPL96589, apertural, side, and apical/side views. Maastrictian, Coon Creek Formation.

Type Material: Holotype: NPL95468 (Figure 9) (apex obscured by matrix), paratype: NPL95469 (Figure 10), Lower Cretaceous, Albian, Fredericksburg Group, Walnut Formation. Another 25 specimens were examined from the type locality.

Dimensions: Holotype: NPL95468 visible height (apex obscured by matrix) 2.4 mm, width 2.6 mm. Paratype: NPL95469 height 3 mm, width 2.5 mm.

Etymology: The specific name: *minutissimus*, notes the diminutive size of this species.

Remarks: In apertural view, *N. minutissimus* resembles some *Polinices* spp. but the inner whorls of *N. minutissimus* have been resorbed and it is clearly a neritimorph. The teleoconch of the holotype retains its outer layer, which is thin and smooth, without any trace of growth lines, although they may have been lost during fossilization. Nearly all other material studied (about 25 specimens) have lost all or most of the outer layer exposing a crystalline inner layer. These small specimens do not appear to be juveniles but are probably adult, as the fauna within the silicified layer in which they are found is composed primarily of small to minute species. In addition, the fauna does not appear to be dwarfed, due possibly to poor environmental conditions, as several of the species, for example *Nerinea acus* Roemer, 1849, are close to the size found in other locations (Stanton, 1947: 80). *Neridomus minutissimus* is closest in appearance to *Neritoma* (*Neridomus*) *delpeyae* Allison, 1955, but that is a larger species: the holotype being 4.8 mm high (Allison 1955: 414), whereas the largest *N. minutissimus* we have examined, the paratype, is only 3 mm high. Also, as mentioned above, the callus on the septum of *N.* (*N.*) *delpeyae* is parallel sided, while that of *N. minutissimus* has a sinuous adapical edge. *Neridomus mccallae* also has a sinuous adapical edge to the septum callus but that is larger, more globular with a significantly broader and thicker callus and a less prominent spire.

Family Otostomidae Bandel, 2008

Genus *Otostoma* d'Archiac, 1859

Type Species: *Natica retzii* Nilsson, 1827 (= *Nerita rugosa* Hoeninghaus, 1831) by typification of *Desmieria* Douvillé, 1904, an unnecessary replacement name. Maastrichtian, Netherlands.

Description: Globose, with depressed spire and rapidly enlarging whorls; ornament narrow collabral ridges or tuberculate spirals; inner lip septum broad, much reducing aperture, with large teeth along margin; outer lip strongly prosocline. (Keen 1960: I282).

Remarks: Pacaud (2009: 350–352) dealt in detail with the problems and confusion concerning the type species and its synonyms. According to Jagt and Kiel (2008: 203) *Nerita rugosa* Hoeninghaus, 1830 is a junior subjective synonym of *Natica retzii* Nilsson, 1827.

Otostoma cattoi new species
(Figures 2–4)

Diagnosis: Small *Otostoma* with about 12 spiral ribs, strongest immediately below suture, crossed by collabral ridges to form a reticulate sculpture; septum convex with four rounded teeth on the septum edge.

Description: Small *Otostoma*; protoconch badly worn on unique holotype; teleoconch hemispherical, about two rapidly expanding, rounded whorls, the last comprising most of the shell; spire low, suture impressed; about 12 strong spiral ribs, wider than the interspaces, the rib immediately below the suture substantially larger, crossed by prominent, evenly spaced, collabral ridges forming a reticulate pattern with small tubercles developed where the transverse ridges cross the spiral ribs. Aperture semi-elliptic; outer lip thick, smooth within; septum smooth, convex; septum edge slightly convex with four evenly spaced, rounded teeth, the largest central.

Type Locality: Temporary exposure on Brushy Creek North housing development, at Great Oaks Drive, north of Sam Bass Road, Round Rock, Williamson County, Texas. GPS: 30°19′46.1994″ N, 97°26′23.9994″ W.

Type Material: Holotype: NPL96587 (Figures 2–4), Lower Cretaceous, Albian, Fredericksburg Group, Edwards Formation.

Dimensions: Holotype: NPL96587, height 5.2 mm, width 5.1 mm.

Etymology: Honoring our good friend and expert paleontologist, Patrick Catto.

Remarks: The unique holotype, preserved as a pseudomorph, is rather worn and has lost the finer detail of its sculpture. Nevertheless, there are sufficient remnants of its distinctive reticulate sculpture to separate it from other *Otostoma* species and to justify its assignment to a new species. The Cretaceous and early Tertiary *Otostoma* species from North America generally have a plainer sculpture on the dorsum; *O. aethes* Squires and Saul, 1993, for example, has several low, collabral swellings and three very low, spiral ribs (Squires and Saul 1993, pp. 261–262, figs. 2–4). *Otostoma lucanus* Saul and Squires, 1997 has numerous, coarse axial ribs (Saul and Squires 1997: 138: 134, figs. 15–18) and *O. atopos* Saul and Squires, 1997 has closely spaced growth rugae (Saul and Squires 1997: 138, 140, figs. 19–21). *Otostoma cattoi* is closest in appearance to *O. apparatum* (Craigin, 1893) but, even allowing for the worn condition of the holotype of *O. cattoi*, there are still clear differences between the two. *Otostoma apparatum* has fewer spiral ribs, six or seven, and the transverse plications are sharply elevated and each divided into three elongated tubercles (Stanton 1947 p. 61, pl. 47, figs. 14, 15), unlike the continuous collabral ridges on *O. cattoi* which are plain apart from the small tubercles at the intersections. Also, *O. apparatum* has six to seven teeth on the septum edge as opposed to four in the case of *O. cattoi*. *Otostoma crispatum*

(Cossmann and Pissarro, 1905) from the middle Eocene, late Lutetian of the Cotentin, France has a reticulate sculpture similar to that of *O. cattoi,* but it only has seven to nine spiral ribs of which three are significantly larger (Cossmann and Pissarro 1905: 109, pl. 18, fig.2); *O. cattoi* has about 12 spiral ribs only one of which is substantially larger.

***Otostoma* sp.**
(Figures 5–6)

Diagnosis: Small *Otostoma* with about 12 beaded, spiral ribs; septum convex with five rounded teeth on the septum edge.

Description: Small *Otostoma*; protoconch worn, possibly globular, exserted; teleoconch hemispherical, about one and a half rapidly expanding, rounded whorls, the last comprising most of the shell, narrow collar below suture; spire low, suture narrow; about 12 low, regular, beaded, spiral ribs, wider than the interspaces. Aperture semi-elliptic; outer lip thin, smooth within; septum smooth, convex; septum edge slightly convex, five rounded teeth, the largest central.

Type Locality: Temporary roadcut exposure during construction of Interstate Highway 10 during 2011, Georgetown, Williamson County, Texas. GPS: 30°37′28.62″ N, 97°41′30.15″ W.

Type Material: Figured specimen: NPL54112 (Figures 5–6), Lower Cretaceous, Albian, Fredericksburg Group, Edwards Formation.

Dimensions: Figured specimen: NPL54112, height 4.0 mm, width 3.8 mm.

Remarks: This species is represented by a single specimen in the NVP collection. It is very small, (4 mm high) and is probably a juvenile. The distinctive ornamentation of beaded, spiral ribs is only visible under high magnification. Other *Otostoma* species with somewhat similar ornamentation, such as *Corsania janus* Woods and Saul, 1986, have a much coarser sculpture of nodose, spiral ribs and an almost flat spire (Woods and Saul 1986, pp. 640–642, fig. 1–4). *Corsania*, incidentally, is now considered to be a junior synonym of *Otostoma* with *Corsania* only representing the adult stage of *Otostoma* (Pacaud 2009, p. 351). The specimen is actually closer in appearance to *O. cattoi* but there is no trace on this specimen of the collabral ridges which are an important characteristic of that species. Although the specimen probably represents an undescribed taxon, we are unwilling to name it as a new species based only on a single, rather poor quality, probably juvenile pseudomorph.

Family Neritidae Rafinesque, 1815
Subfamily Neritinae Rafinesque, 1815
Genus *Pseudodostia* Symonds, 2006

Type Species: *Nerita aperta* J. de C. Sowerby, 1823, by original designation. Late Eocene, Headon Hill Formation, probably from Colwell Bay, Isle of Wight, England.

Description: Spire depressed; outer surface of teleoconch almost smooth or with spiral ridges; septum edge with a prominent tooth at about one quarter of the distance from the apical end and smaller denticles abapical, and in some cases, adapical to it, outer lip somewhat thickened, usually with fine lirae within; operculum semicircular with a ridge on the inner surface running from the nucleus to a prominent medial tooth on the columellar side; a double apophysis, the ventral being a thickened, arcuate ridge, the dorsal an elongate peg (Symonds, 2006: 27).

Remarks: *Pseudodostia* differs from *Nerita* sensu stricto and all other generally recognized subgenera by the dentate nature of the teeth on the septum edge. *Pseudodostia* species are known from the early Eocene, Ypresian of France with *P. custugensis* (Doncieux, 1908) to the late Eocene, Priabonian of England with *P. aperta* (J. de C. Sowerby, 1823), with the majority of species having been described from the Cuisian and Lutetian of Europe.

***Pseudodostia lisbonensis* new species**
(Figures 14–16)

Diagnosis: Small *Pseudodostia*, with numerous low, spiral ridges crossed by frequent, collabral growth lines; septum edge with about four denticles abapical to the main tooth; outer lip thick with distinctive lirae within.

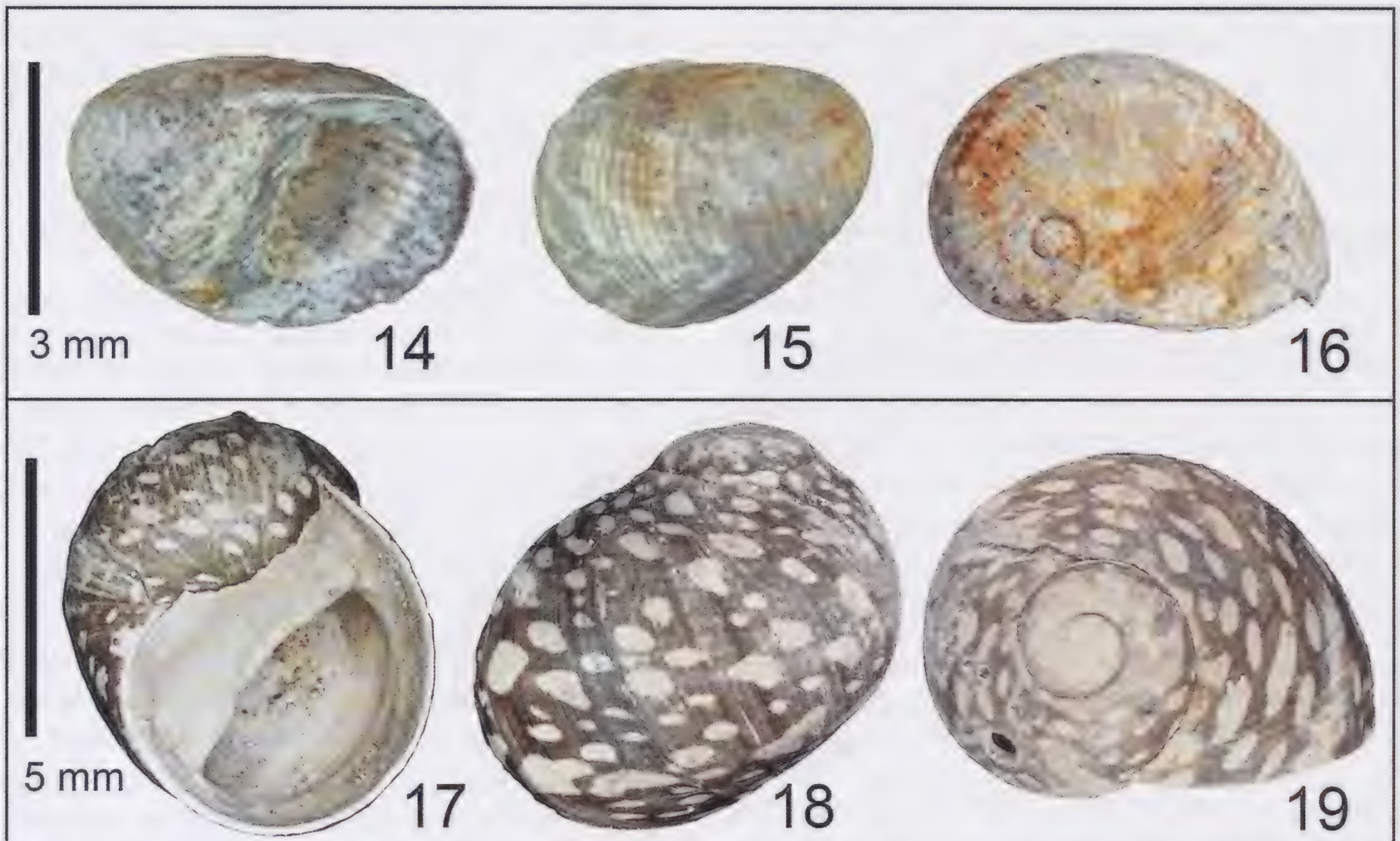
Description: Small *Pseudodostia*; protoconch worn, set below the last teleoconch whorl, circa one and a half whorls, globular, tip damaged, remaining whorl inflated, shining. Teleoconch one and a half whorls, broadly obovate in adapertural view, posterior narrow, subangular; spire depressed; whorls rounded, suture impressed, about twenty low, regular, indistinct spiral ridges, narrower than the interspaces, crossed by numerous, prominent, evenly spaced, collabral growth lines forming a distinctive reticulate pattern on dorsum. Aperture broad, semicircular; septum broad, surface rough but polished, edge slightly concave with large, prominent tooth toward adapical end, one small denticle adapical to it, four small, irregular, widely spaced denticles abapical to it; apertural tooth a narrow ridge below abapical end of septum; outer lip considerably thickened within; ten clearly defined lirae, the posterior-most much larger. Color pattern broad, wavy, pale lines on a purple brown background.

Type Locality: Little Stave Creek downstream from Gosport Sand lens, at first occurrence of sand lens in Lisbon Formation, Clarke County, Alabama. GPS: 31° 33′ 9.4998″ N, 87°54′40.5786″ W.

Type Material: Holotype: NPL96588 (Figures 14–16), Eocene, Claiborne Group (Bartonian), upper Lisbon Formation.

Dimensions: Holotype: NPL96588, height 3.3 mm, width 4.0 mm.

Remarks: *Pseudodostia* are relatively common in the Eocene of Europe, with over ten species recorded.



Figures 14–25. New species of fossil Neritidae. **14–16. *Pseudodostia lisbonensis* new species (1–3)** holotype NPL96588, apertural, rear, apical views. Eocene, Lisbon Formation. **17–19. *Clithon duomillias* new species,** holotype NPL95466, apertural, rear, and apical views. Eocene, Cook Mountain Formation, Landrum Member. **20–22. *Clithon lisae* new species**, holotype NPL95465, apertural, rear and apical views. Eocene, Cook Mountain Formation, Wheelock Member. **23–25. *Clithon traceyi* new species,** holotype NPL95463, apertural and rear views; paratype NPL95464, apical view. Eocene, Cook Mountain Formation, Stone City Member.

Pseudodostia lisbonensis can be readily distinguished from all of them by its distinctive ornamentation of collabral and spiral ridges. European species either have a smooth exterior, *P. baylei* (Vasseur, 1882), for example, from the middle Eocene (Bartonian), Faluns de Bois-Gouët; Saffré, Bois-Gouët, Loire-Atlantique, France or, more often, prominent spiral ribs, usually at least three in number, *P. tricarinata* (Lamarck, 1804), a widespread and common species, being a good example. Most lack collabral ridges and on the few species that do have them, such as *P. calcarata* (Cossmann and Pissarro, 1905) from the Cotentin, France, the growth lines are much finer than the spiral ribs and they do not form a reticulate pattern.

Pseudodostia species are less common in the Americas but several taxa have been described that have all the characteristics of this genus. For example, *Nerita (Theliostyla) triangulata* Gabb, 1869, from the Eocene of the Pacific coast of North America, as described and figured by Squires (1992, pp. 325–326, figs. 2–9), appears to belong in this genus. In particular, the large tooth toward the adapical end of the septum edge, shown clearly in figure 3 on page 325 and described on page 326, is an important characteristic of *Pseudodostia,* but is not present on *Nerita albicilla* Linnaeus, 1758, the type species of *Theliostyla*. However, *N. (T.) triangulata* can be readily distinguished from *P. lisbonensis* by the presence of prominent, spiral ribs, when compared to the rather indistinct spiral ridges on *P. lisbonensis* and by the small tubercles on the surface of the septum of *N. (T.) triangulate,* which are lacking on *P. lisbonensis*. *Nerita reticulirata* Dockery, 1993 from the Campanian, Coffee Sand Formation of northeastern Mississippi, also has the characteristics of *Pseudodostia* (Dockery 1993: 43, pl. 1, figs. 18–20) but, again it can be separated from *P. lisbonensis* by its prominent, beaded, spiral ribs. The presence of numerous, narrow, well-defined, spiral ribs on *P. lisbonensis* also serves to separate it from *N. (T.) kennedyi* Squires and Saul 2002 (pp. 184–187, figs. 31–34), from the Eocene, Santiago Formation, southern California, which also appears to be a *Pseudodostia*.

Etymology: Noting the occurrence in the Lisbon Formation.

Genus *Clithon* Montfort, 1810

Type Species: *Nerita corona* Linnaeus (1758: 777, nr. 629), by original designation. Recent, fresh to brackish water, eastern Indian Ocean to the Southwestern Pacific.

Description: Small spire and large body whorl, some species with a subsutural row of spines; labial area smooth with one or more teeth on the margin; operculum smooth or bearing minute granules on the exterior surface, inner side with two apophyses connected by a calcareous callus (Symonds 2006: 31).

Remarks: Although proposed as a genus by Montfort (1810: 327), Baker (1923, pp. 154–156), on studying characteristics of the radula, considered *Clithon* to be a subgenus of *Theodoxus* Montfort, 1810. He was followed by Keen (1960: I285) and Vaught (1989: 13). However, Wenz (1938, pp. 422–423) recognized *Clithon* as a distinct genus and his interpretation was confirmed by Holthuis (1995: 184), on the basis of anatomical data from Recent species. We follow Wenz, Holthuis, Symonds (2006: 31) and Eichhorst (2016: 154) in regarding *Clithon* as a separate genus.

Wenz (1938: 423) regarded *Pictoneritina* Iredale, 1936 (type species *Neritina oualaniensis* Lesson, 1831) as a subgenus of *Clithon*. Subsequent authors (including Symonds 2006; Symonds et al. 2018 and Vrinat 2019) followed Wenz in placing *Clithon* species from the Tertiary of Europe in subgenus *Pictoneritina.* However, Holthuis (1995, pp. 196, 197), after dissection of Recent *Clithon*, concluded that the type species of *Clithon* and *Pictoneritina* were too similar anatomically to justify retaining *Pictoneritina* as a subgenus of *Clithon* and relegated it to a junior synonym. She was followed by Eichhorst (2016: 154) who agreed that *Pictoneritina* should not be used for Recent species, whilst conceding that it might have more relevance for fossil species. One of the distinguishing characteristics of *Pictoneritina*, as currently applied to fossil species, is the presence of one large and several small teeth on the septum edge (Keen 1960, p. I285). Whilst most European species of fossil *Clithon* possess this characteristic, the Eocene species described below do not. Accordingly, regardless of whether *Pictoneritina* should validly be used for fossil species of *Clithon*, it does not apply to the species described herein.

Clithon traceyi new species
(Figures 23–25)

Diagnosis: Medium-sized *Clithon*, spire low, whorls slightly concave below the suture; septum smooth; edge with one obscure, broad tooth, two or three very small, obscure denticles adapical to it, about five small denticles abapical to it. Color pattern pale blotches, sometimes merging into spiral bands, on dark brown background.

Description: Medium-sized *Clithon*; protoconch of one flattened whorl set below the apical surface of the first teleoconch whorl resulting in a deep sutural groove between the embryonic and adult whorls. Teleoconch smooth, glossy, about two-and-a-quarter whorls, semi-globular, spire low; whorls evenly convex with slight concavity below suture, which is sharp and well defined. Aperture oblique, semi-circular; septum slightly concave, smooth; septum edge concave in center, one broad tooth about one third of distance from adapical end, adapical to it are two to four small denticles, sometimes almost effaced; abapical to it a small gap then about five small, well defined denticles reducing in size abapically; no apertural tooth; outer lip thin, evenly rounded, smooth, terminating in narrow gutter at adapical end. Color pattern pale blotches of irregular size and shape on dark brown background; blotches coalescing into one or more pale, spiral bands on some specimens.

Type Locality: Bank of Trinity River, 1.45 km upstream of abandoned Alabama Ferry, Houston County, Texas. GPS: 31°15′10.4688″ N, 95°43′24.6678″ W.

Type Material: Holotype: NPL95463 (Figures 23, 24), paratype: NPL95464 (Figure 25), paratype: NPL98441, Eocene, Lutetian, Claiborne Group (Lutetian), Cook Mountain Formation, Stone City Member.

Dimensions: Holotype: NPL9546, height 6.5 mm, width 6.0 mm., paratype: NPL95464, height 7.1 mm, width 6.6 mm, unfigured paratype NPL98441, height 6.9 mm, width 7.0 mm.

Other Material Examined: Twelve additional specimens were also examined from the upper beds (channel deposits) of the type locality, and one specimen from the lower beds (coarse sandstone deposits) adjacent to the type locality, GPS: 31°15′10.4688″ N, 95°43′26.8212″ W. All specimens are deposited in the senior author's collection.

Etymology: Honoring our good friend and molluscan expert, Steven Tracey.

Remarks: Fourteen specimens were available for examination, the primary character showing variation in the strength of the denticles, those adapical to the gap sometimes so faint as to be almost absent. The first denticle abapical to the gap usually but not always duplex in character, the remaining strong in character. Adult specimens have a white band behind the outer lip, the ends of which connect with the septum edge. The one specimen from the secondary sandstone bed (Stone City Member) is about twice the size of the specimens from the channel deposit, has the same color pattern, and although mostly obscured by apertural matrix, appears to have more, and more similarly sized denticles; the specimen is missing most of the outer shell in the vicinity of the protoconch.

Clithon lisae new species
(Figures 20–22)

Diagnosis: Medium size *Clithon*, spire low, whorls concave below the suture; septum smooth, narrow at adapical end; edge with one broad, rounded tooth, two small denticles adapical to it, one large and about eight small denticles abapical to it. Color pattern pale blotches on dark brown background.

Description: Medium size *Clithon*; protoconch of one flattened whorl set at the level of the apical surface of the first teleoconch whorl resulting in a channel between the embryonic and adult whorls. Teleoconch smooth, glossy, about two-and-a-quarter whorls, semiglobular, spire low; whorls evenly convex apart from pronounced concavity below suture which is impressed and sharply defined. Aperture oblique, semi-circular; septum concave, narrow at adapical end, smooth; septum edge slightly concave in center, one broad rounded tooth about one third of distance from adapical end, adapical to it two small denticles; abapically one fairly large and eight smaller denticles in central concavity, becoming progressively weaker; outer lip thin, evenly rounded, smooth, terminating in short, narrow gutter at adapical end. Color pattern pale blotches of irregular size and shape on dark brown background.

Type Locality: Bank of the Little Brazos River, downstream of Highway 21 bridge, Brazos County, Texas. GPS: 30°38′18.2184″ N, 96°30′57.9198″ W.

Type Material: Holotype: NPL95465 (Figures 20–22), Eocene, Lutetian, Claiborne Group, Cook Mountain Formation, Wheelock Member.

Dimensions: Holotype: NPL95465, height 5.4 mm, width 5.7 mm.

Remarks: For a comparison with the two other *Clithon* species from the Cook Mountain Formation see below.

Etymology: Honoring Lisa Boucher, curator and director of the Non-vertebrate Paleontology Laboratory, Jackson School of Geosciences, The University of Texas at Austin.

Clithon duomillias new species
(Figures 17–19)

Diagnosis: Medium size *Clithon*, spire low, whorls slightly concave below the suture; septum smooth; edge concave in center with about seven distinct, rounded teeth decreasing in size abapically. Color pattern of pale blotches on dark brown background.

Description: Medium size *Clithon*; protoconch of one flattened whorl set at level of apical surface of the first teleoconch whorl, resulting in a channel between embryonic and adult whorls. First teleoconch whorl begins weakly, centrally carinate, the carina spiraling into the suture after the first half whorl. Teleoconch smooth, apart from numerous fine, collabral growth lines, glossy, about two-and-a-quarter whorls, semiglobular, whorls evenly convex with slight concavity below suture, which is impressed, sharply defined. Aperture oblique, semi-circular; septum smooth; septum edge concave in center, series of about seven distinct, rounded teeth, the adapical first two very weak, extending from adapical end of septum to abapical end of central concavity, decreasing slightly in size abapically; apertural tooth a low ridge below abapical end of septum; outer lip thin, evenly rounded, smooth. Color pattern pale blotches of irregular size and shape on dark brown background.

Type Locality: Two Mile Creek, bluffs 0.8 km downstream of branch crossing Old San Antonio Road, 0.64 km west of Interstate Highway 45, Leon County, Texas. GPS: 31°5′43.9584″N, 95°57′9.7488″ W.

Type Material: Holotype: NPL95466 (Figures 17–19), Eocene, Lutetian, Claiborne Group, Cook Mountain Formation, Landrum Member.

Dimensions: Holotype: NPL95466, height 7.6 mm, width 8.0 mm.

Etymology: The specific name *duo* (Latin, two), *millias* (Latin, mile), referring to the locality, Two Mile Creek where the specimen was found.

Remarks: The three *Clithon* species described above are rather similar in both shell morphology and color pattern and it may well be that they represent the evolution of *C. traceyi* in the Stone City Member, through *C. lisae* in the Wheelock Member to *C. duomillias* in the Landrum Member. However, all three can be separated by differences in morphology, particularly the denticulation on the septum edge and the shape of the shell, with the younger species becoming progressively less globular. Although *C. lisae* and *C. duomillias* are known only from their holotypes, we have examined 14 specimens of *C. traceyi* from the type locality and they show very little intraspecific variation, none being noticeably closer than the others in appearance to *C. lisae* or *C. duomillias.* In the circumstances, we consider that they merit description as separate species rather than merely being regarded as variations of a single species.

***Clithon cooncreekense* new species**
(Figures 11–13)

Diagnosis: Large *Clithon*, spire not exserted, exceeded in height and partially obscured by final whorl; septum edge with single small protuberance about one third of distance from adapical end, otherwise smooth; color pattern brown transverse lines which vary in spiral bands.

Description: Large *Clithon*, protoconch completely obscured by first teleoconch whorl. Teleoconch smooth, glossy, about two whorls, very slight concavity develops after first whorl, semiglobular, spire not exserted; body whorl extended adapically higher than and partially obscuring apex, suture impressed, clearly defined. Aperture oblique, semi-circular; septum broad, smooth; septum edge slightly concave, smooth apart from a slight protuberance about one third of distance from adapical end and a second much weaker one at abapical end; apertural tooth not visible; outer lip smooth, evenly rounded, partially missing in only known specimen. Color pattern brown, transverse lines; on the adapical part of body whorl these are fine, closely packed, merging adapically with brown background; on central part of whorl lines are broader, widely spaced, wavey, forming chevrons in places, on pale background, below which is pale spiral band without lines; on lowest part of whorl broad lines on pale background become narrower abapically, eventually merging with brown background.

Type Locality: Coon Creek. Near Adamsville, McNairy County, Tennessee. (Coon Creek Formation type locality). GPS: 35°20'12.5586" N, 88°26'17.6892" W.

Type Material: Holotype: NPL96589 (Figures 11–13), Upper Cretaceous, Maastrichtian, Coon Creek Formation.

Dimensions: Holotype: NPL96589, height 13.3 mm, width 11.4 mm.

Etymology: Noting the occurrence in the Coon Creek Formation.

Remarks: The above description is based on the unique holotype and accordingly takes no account of any intraspecific variation that may occur. In particular, by analogy with species such as *C. inequidentatum* (Récluz, 1850) from the middle Eocene (Bartonian), Faluns de Bois- Gouët; Bois-Gouët, Saffré, Loire-Atlantique, France, which has a color pattern that is quite variable but always involves transverse lines, it is likely that *C. cooncreekense* also has a variable pattern.

As noted above, most European *Clithon* fit the diagnosis of subgenus *Pictoneritina*, including a large tooth toward the adapical end of the septum edge and several small teeth abapical to it. The *Clithon* species described above do not have this feature, which separates them from those European *Clithon* with a similar color pattern.

A few American Neritidae have some similarity to the *Clithon* species described above despite not being in the same genus. The "*Neritina* sp." briefly described and figured by Dockery (1993: 44, pl. 4, figs. 3 and 4) from the Ripley Formation of Union County, Mississippi, has a smooth, glossy dorsum with a color pattern of light spots on a dark background and could, from the figures, be either a *Neritina* or *Clithon* species. However, a "non-denticulate, rounded, columellar septum" in Dockery's diagnosis, fits neither *Neritina* nor *Clithon*. The fact that it is described as edentate clearly separates it from all the *Clithon* species described herein. *Nerita* (*Bajanerita*?) *larix* Saul and Squires, 1997, from the Eocene, Crescent Formation, Thurston County, Washington, also has a smooth surface and a color pattern which could belong to a *Clithon* (Saul and Squires 1997, pp. 134, 136, figs. 9, 10) but the narrow aperture with the convex edge to the septum and four equal, widely spaced teeth is quite unlike *Clithon* and much closer to *Bajanerita*. *Theodoxus domicilium* Garvie, 1996 from the Eocene, Reklaw Formation of Texas has a glossy surface and distinctive color pattern (Garvie 1996: 47, pl. 9, fig. 23) but the straight, edentate septum edge confirms it as *Theodoxus* not *Clithon*.

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LITERATURE CITED

Aldrich, T.H. 1911. New Eocene fossils from the southern Gulf states. Bulletins of American Paleontology 5(22): 1–25.

Allison, E.C. 1955. Middle Cretaceous Gastropoda from Punta China, Baja California, Mexico. Journal of Paleontology 29: 400–432.

Baker, H.B. 1923. Notes on the radula of the Neritidae. Proceedings of the Academy of Natural Sciences of Philadelphia 75: 117–178.

Bandel, K. 2001. The history of *Theodoxus* and *Neritina* connected with description and systematic evaluation of

related Neritimorpha (Gastropoda). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 85: 65–164.

Bandel, K. 2008. Operculum shape and construction of some fossil Neritimorpha (Gastropoda) compared to those of modern species of the subclass. Vita Malacologica 7: 19–36.

Bandel, K. and J. Frýda. 1999. Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with description of some new taxa. Geologica et Palaeontologica 33: 219–235.

Barnes, V.E. (director). 1982. Geologic atlas of Texas. University of Texas at Austin, Bureau of Economic Geology, scale 1:250,000. Robert Hamilton Cuyler memorial edition. 1 sheet, 9 p.

Bouchet, P., J.-P., B. Rocroi, A. Hausdorf, Y. Kaim, A. Kano, P. Nützel, P. Parkhaev, M. Schrödl, and E.E. Strong. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61(1–2): 1–526.

Cossmann, M. 1907. Le Barrémien supérieur à faciès Urgonien de Brouzet-lez-Alais (Gard). Description des Gastropodes et Pélécypodes. Mémoires de la Société Géologique de France, sérial 15, tome 2, mémoire 37: 6–42

Cossmann M. and G. Pissarro. 1905. Faune éocénique du Cotentin (Mollusques). 6è article. Bulletin de la Société Géologique de Normandie 24: 51–122.

Cox, L.R., and W.J. Arkell. 1950. A survey of the mollusca of the British Great Oolite series. Primarily a nomenclatorial revision of the monographs by Morris and Lycett (1851–55). Lycett (1863) and Blake (1905–1907). Part II. London: Palaeontographical Society CIII. xiv–xxiv, 49–105.

Craigin, F.W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. Texas Geological Survey, Annual Report 4(2): 139–246.

D'Archiac, A. 1859. Note sur le genre *Otostoma.* Bulletin de la Société Géologique de France 2(16): 871–879.

Dockery, D.T. III. 1993. The Streptoneuran gastropods, exclusive of the Stenoglossa, of the Coffee Sand (Campanian) of northeastern Mississippi. Mississippi Department of Environmental Quality Office of Geology, Bulletin 129: 1–191.

Doncieux, L. 1908. Catalogue descriptif des fossils nummulitiques de l'Aude et de l'Hérault. Annales de l'Université de Lyon 22: 1–288.

Douvillé, H. 1904. Mission scientifique en Perse de J. de Morgan, tome III, études géologiques, partie IV: paléontologie, mollusques fossiles. Leroux, Paris, pp. 191–380, pls. 25–50.

Eichhorst, T.E. 2016. Neritidae of the World. Volume 1. Conchbooks, Harxhein. 695 pp.

Fischer, P. 1880–1887. Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles suivi d'un Appendice sur les Brachiopodes par D. P. Oehlert. Avec 23 planches contenant 600 figures dessinées par S. P. Woodward. Paris: F. Savy. Published in 11 parts (fascicules). Part 8: 689–784, 1885.

Gabb, W.M. 1869. Cretaceous and Tertiary fossils. Geological Survey of California. Vol. 2. Palaeontology. Caxton Press, Philadelphia, 299 pp.

Gardner, J.A. 1957. Little Stave Creek, Alabama-paleoecologic study, *in* Ladd, H.S. (ed.), Treatise on Marine Ecology and Paleoecology. Vol. 2. Paleoecology. Geological Society of America, Memoir 67: 573–587.

Garvie, C. L. 1996. The molluscan macrofauna of the Reklaw Formation, Marquez Member (Eocene: Lower Claibornian) in Texas. Bulletins of American Paleontology 111(352): 1–177.

Garvie, C.L., J.L. Goedert, and A.W. Janssen. 2020. Paleogene and Late Cretaceous Pteropoda (Mollusca, Gastropoda, Heterobranchia) from North America. Zootaxa 4782: 1–115.

Golikov, A.M. and Y.I. Starobogatov. 1975. Systematics of prosobranch gastropods. Malacologia 15(1): 185–232.

Groves, L.T. and R.L. Squires. 2021. Checklist of California Paleogene–Neogene marine Mollusca since Keen and Bentson (1944). Paleobios 38: 1–360.

Hoeninghaus, F.W. 1831. Versuch einer geognostischen Eintheilung seiner Versteinerung-Sammlung (Dritter Theil. Tertiär-Gebirge). Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde. Verlag von Georg Reichard, Heidelberg. Zweiter Jahrgang, 1831, pp. 132–170.

Holthuis, B. 1995. Evolution between marine and freshwater habitats: a case study of the gastropod suborder Neritopsina [Ph.D. dissertation]: University of Washington, 286p.

Insole, A. and B. Daley. 1985. A revision of the lithostratigraphical nomenclature of the Late Eocene and early Oligocene strata of the Hampshire Basin, southern England. Tertiary Research 7(3): 67–100.

Iredale, T. 1936. Australian molluscan notes, No. 2, Records of the Australian Museum 19(5): 267–340.

Jagt, J.W.M. and S. Kiel. 2008. The operculum of *Otostoma retzii* (Nilsson, 1827) (Gastropoda, Neritidae: Late Cretaceous) and its phylogenetic significance. Journal of Paleontology 82(1): 201–205.

Kase, T. 1984. Early Cretaceous marine and brackish-water Gastropoda from Japan. National Science Museum Monographs, Tokyo, 199 pp.

Keen, M. 1960. Systematic Descriptions, *in*: Moore, R. (ed.), Treatise on Invertebrate Palaeontology. Pt. I. Mollusca 1. Lawrence, Geological Society of America and University of Kansas Press: I1–I351.

Lamarck, J.B.P.A. de. 1804. Suite des mémoires sur les fossiles des environs de Paris. Annales du Muséum d'Histoire Naturelle 5: 28–36; 91–98; 179–188; 237–245.

Lamarck, J.B.P.A. de M. de. 1815–1822**.** Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux &c**.** Deterville, Paris. 1–462; Tome 2 (1816).

Lesson, R.P. 1830–1831. Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de la Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Zoologie 2(1): 1–471.

Linnaeus, C. von. 1758. Systema naturae per regne tria naturae. Editio decima reformata. Vol. 1. Regum Animale. Stockholm, iii+824 pp.

Lozo, F.E., H.F. Nelson, K. Young, O.B. Shelburne, and J.R. Sandidge. 1959. Symposium on Edwards Limestone in central Texas. The University of Texas Bureau of Economic Geology, Publication 5905: 235 pp.

McCall, L., J. Sprinkle, and A. Molineux. 2008. Spectacularly preserved, mollusc-dominated fauna from a cavity layer in the Lower Cretaceous Edwards Formation, central Texas. Gulf Coast Association of Geological Societies, Transactions 5: 683–694.

Montfort, P.D. 1810. Conchyliologie systématique et classification méthodique des coquilles. Vol. 2. Schoell, Paris, 176 pp.

Mörch, O.A.L. 1852. Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra et Gadea Comes de Yoldi, Regis Daniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Tertii Eques. Fasc. 1, Cephalophora. Copenhagen, 170 pp.

Morris, J. 1849. On *Neritoma*, a fossil genus of gasteropodous mollusks allied to *Nerita*. Quarterly Journal of the Geological Society of London 5: 332–335.

Morris, F.G.S. and J. Lycett. 1851–1855. A monograph of the Mollusca from the Great Oolite chiefly from Minchinhampton and the coast of Yorkshire. Palaeontographical Society, London, 130 pp.

Nilsson, S. 1827. Petrificata suecana formationis Cretaceae, descripta et iconibus illustrata. Pars Prior, Vertebrata et Mollusca sistens. London, 29 pp.

Pacaud, J.-M. 2009. Révision des mollusques du Danien (Paléocène inférieur) du Bassin de Paris. 2. Gastropoda: Neritimorpha. Revue de Paléobiologie 28(2): 349–369.

Rafinesque, C.S. 1815. Analyse de la Nature ou Tableau de L'Univers et des Corps Organises. Privately published, Palermo, pp. 138–149.

Récluz, C.A. 1850. Des Neritines, section des Crepidiformes (sandaliformes; Mitrulae, Menke, Synop. moll 1830). Journal de Conchyliologie 1: 58–72.

Richards, H.G. 1946. A gastropod of the genus *Velates* from the Florida Eocene. Proceedings of the Academy of Natural Sciences of Philadelphia 177: 6 pp.

Roemer, C.F. 1849. Texas. Mit besonderer Rücksicht auf deutsche Auswanderung und die physischen Verhältnisse des Jandes nach eigener Beobachtung Geschildert von Dr Ferdinand ROEMER. Adolph Marcus, Bonn. 464 pp.

Russell, E.E. and W.S. Parks. 1975. Stratigraphy of the outcropping Upper Cretaceous, Paleocene, and lower Eocene in western Tennessee (including descriptions of younger fluvial deposits). Tennessee Division of Geology, Bulletin 75: A1–A65, B1–B53.

Saul, L.R. and R.L. Squires, 1997. New species of neritid gastropods from Cretaceous and lower Cenozoic strata of the Pacific slope of North America. The Veliger 40(2): 131–147.

Sowerby, J. de C. 1823–1826. The Mineral Conchology of Great Britain, or coloured figures and descriptions of those remains of testaceous Animals or Shells, which have been preserved at various times, and depths in the earth. London 4–7(67–113), 484 pp.

Squires, R.L. 1992. New morphological and geographic data on the neritid Gastropod *Nerita (Theiliostyla) triangulata* Gabb, 1869, from the Eocene of the Pacific Coast of North America. The Veliger 35(4): 323–329.

Squires, R.L. and L.R. Saul. 1993. A new species of *Otostoma* (Gastropoda: Neritidae) from near Dip Creek, Lake Nacimiento, California. The Veliger 36(3): 259–264.

Squires, R.L. and L.R. Saul. 2002. New early Late Cretaceous (Cenomanian) mollusks from Oregon. Journal of Paleontology 76(1): 43–51.

Stanton, T.W. 1947. Studies of some Comanche pelecypods and gastropods. U.S. Geological Survey Professional Paper 211: 1–256.

Symonds, M.F. 2006. The Neritidae of the Solent Group (late Eocene and early Oligocene) of the Hampshire Basin. Cainozoic Research 4(12-2): 27–39.

Symonds, M.F. O. Gain, and L. Bellard, 2018. The Neritidae (Mollusca, Gastropoda, Neritimorpha) from the middle Eocene of the Cotentin (Manche, France). Carnets de Voyages Paléontologiques dans le Bassin Anglo-Parisiene 4: 47–86.

Tracey, S., J.A. Todd, and D.H. Erwin. 1993. Mollusca: Gastropoda *in* Benton, M.J. (ed.), The Fossil Record 2. Chapman and Hall, London, pp. 131–167.

Vasseur, G. 1882. Recherches géologiques sur les terrains tertiaires de la France occidentale. Atlas paléontologique. Quinsac, Toulouse, 19 pp.

Vaught, K.C. 1989. A classification of the living Mollusca. American Malacologists, Melbourne, Florida, 195 pp.

Vermeij, G.J. and R.W. Portell. 2013. New fossil records of Neritidae (Gastropoda) from Florida, U.S.A. Cainozoic Research, 10(1–2): 53–57.

Vrinat, X. 2019. The smooth-shelled Neritidae from the Ypresian of the Paris basin. Cainozoic Research 19(1): 45–78.

Wade, B. 1926. The fauna of the Ripley Formation on Coon Creek, Tennessee. United States Geological Survey Professional Paper 137: 1–272.

Wenz, W. 1938–1944. Teil 1: Allgemeiner Teil und Prosobranchia, *in*. Schindewolf, O.H. (ed.), Handbuch der Paläozoologie, Band 6, Gastropoda. Borntraeger, Berlin. xii+1639 pp. Lieferung 3: 241–480 (1938).

Wingard, G.L. 1993. A detailed taxonomy of Upper Cretaceous and lower Tertiary Crassatellidae in eastern North America; an example of the nature of extinction. United States Geological Survey Professional Paper 1535: 1–131.

Woods, A.J.C. and L.R. Saul. 1986. New Neritidae from southwestern North America. Journal of Paleontology 60: 636 – 655.

Zvonareva, S., Y. Kantor, X. Li, and T. Britayev. 2015. Long-term monitoring of Gastropoda (Mollusca) fauna in planted mangroves in central Vietnam. Zoological Studies 54: e39.

New distributional record of pen shell *Atrina hystrix* (Hanley, 1858) (Bivalvia: Pinnidae) from Chennai coast, India

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ABSTRACT

In the present study, we have reported for the first time, occurrence of *Atrina hystrix* (Hanley, 1858) from India. Earlier, the distribution range for *A. hystrix* was limited to Indo-West Pacific areas of the Philippines, Indonesia, Thailand, and New Caledonia. A single specimen was collected from Neelankarai artisanal fishing village, Chennai, India, while examining the set gill-net bycatch operated along the coast. The identity of the specimen was ascertained following key morphological characters. A brief morphological description with an outline of the internal valve is presented in this article. Further, a morphological comparison of *A. hystrix* was made with closely related *Atrina* spp., *A. pectinata*, and *A. vexillum*. Molecular studies based on cytochrome oxidase subunit I gene sequence showed 98.2% similarity with previously reported *A. hystrix* from Philippines. The maximum likelihood-based phylogenetic tree revealed that *A. hystrix* forms a sister clade to *A. vexilum* supported by a high bootstrap value. The genetic divergence analysis showed <2% between *A. hystrix*, 25–29% distance among the congeners *A. vexillum*, *A. pectinata*, and >35% with *Pinna* spp.

Additional keywords: Pinnidae, Bivalve, India, DNA barcoding, integrative taxonomy

INTRODUCTION

The species of the family Pinnidae Leach, 1819 are filter feeders, commonly known as pen or fan shells. The shells of this family encompass a group of commercially important subtidal and coastal species (Lemer et al., 2014) found across the world's oceans. These animals are harvested for human consumption in many regions of the world. Pinnid species also form a critical element in several marine ecosystems, inhabiting the sandy substrate of seagrass beds, lagoons, and coral reefs, where they can aggregate in large densities (Rosewater, 1961). Pen shells are yellow-brown to dark-brown colored triangular bivalves with a sharp posterior margin and a tapering anterior end. The shell partially or completely buries itself from the pointed anterior end in the sandy or muddy substratum, or is attached by byssus to reef rocks (Morton, 1998).

The family Pinnidae contains two recognized genera including 58 species occurring in coastal and oceanic waters worldwide (Turner and Rosewater, 1958; Rosewater, 1961; Schultz and Huber, 2013, Lemer et al., 2014). The genera *Atrina and Pinna* comprise 30 and 28 species respectively (WoRMS, accessed on 1 August 2022). In the Indian waters, 12 species belonging to all two genera have been hitherto recorded including *Atrina vexillum* (Born, 1778), *A. pectinata* (Linnaeus, 1767), *A. chinensis* (Deshayes, 1841), *A. serrata* G.B. Sowerby I, 1825, *Pinna bicolor* Gmelin, 1791, *P. incurva* Gmelin, 1791, *P. deltodes* Menke, 1843, *P. atropurpurea* G.B. Sowerby I, 1825, *P. muricata* Linnaeus, 1758, *P. trigonium* Dunker, 1852, *P. linguafelis* (Habe, 1953), and *P. saccata* Linnaeus, 1758 (Nagabhushanam and Rao, 1972; Ramakrishna and Dey, 2010; Balaji et al., 2012; Gopalakrishnan et al., 2012; Ravinesh and Bijukumar, 2015; Stella, et al., 2015; Vaitheeswaran and Malathi, 2015). However, the above records need to be validated, because records of a few species (such as *A. chinensis*, *P. trigonium*, *P. deltodes*) were either published in predatory journals or in checklists alone, with no citation of original literature and of voucher specimens.

According to Rosewater (1982), key identification characters of pen shells include those present in the internal surface of the valves. The diagnostic characters for *Pinna* Linnaeus, 1758 species include an internal nacreous area divided into dorsal and ventral lobes by an antero-posteriorly directed sulcus. If the nacreous area entirely occupies the anterior internal valve surface, species belong to *Atrina* Grey, 1842.

In the present study, we have reported a new distributional record for *Atrina hystrix* (Hanley, 1858) from the Chennai coast, India, making it the fifth species of the genus *Atrina* found in Indian waters. We have provided a description of the anatomy and morphology of the species with a comparison with congeners. Also, we have performed cytochrome oxidase subunit I (COI) based molecular identification to ascertain the identity of the specimen.

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MATERIALS AND METHODS

Sample Collection and Morphological Examination: An individual specimen was collected from the Neelankarai artisanal fishing village, Chennai (12°57′19″ N, 80°15′46″ E), while examining the set gill-net bycatch on 18 May 2022. We took a photograph of the specimen in the field and then the specimen was brought in an ice box to the marine biology facility at the Centre for Climate Change Studies, Sathyabama Institute of Science and Technology, Chennai for further examination. Morphological examination and terminology in this paper were used following Scheltema (1983).

For study and record-keeping of morphological characters, photographs of the specimen were taken showing its external and internal shell surfaces. Meristic characters were recorded using a Vernier caliper as follows: length of anterior to posterior adductor muscle length (APAML), posterior adductor muscle to posterior shell margin (PAMPSM), dorsal posterior margin length (DPML), dorsal margin length (DML), width (WL), total length (TL), posterior adductor muscle to posterior dorsal nacreous layer (PAMPDNL), and dorsal nacreous length (DNL). After morphological examination, a portion of adductor muscle was stored in 95% ethanol for molecular studies.

Molecular Identification and Phylogeny: Total genomic DNA was extracted from ethanol-preserved adductor muscle using a commercial kit (OMEGA BIO-TEK E.Z.N.A. Blood & Tissue DNA Kit, USA) following the manufacturer's protocol. PCR amplification for the cytochrome oxidase subunit I (COI) gene was carried out using LCO-1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO-2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′) primers (Folmer et al., 1994). Each PCR contained 12.5µL 2X PCR master mix (Amplicon, Denmark), 2.5µL each of the two primers (10nM), and 2.5µL of template DNA and nuclease-free water to make a final volume of 25µL. PCR conditions were as follows: initial denaturation at 95°C for 10 min, 35 cycles of 95°C for 45 sec, 45°C for 45 sec, and 72°C for 1 min, and final extension at 72°C for 10 min.

Figure 1. *Atrina hystrix*, shell. A. External view B. Internal view.

PCR products were then visualized on 1% agarose and products with the high-intensity band were sequenced with ABI Prism 3730 Genetic Analyzer based on Big-Dye® Terminator Chemistry.

Chromatograms were visualized in BioEdit (Hall, 1999) and contig was prepared. The COI gene sequence for *A. hystrix* is deposited in NCBI GenBank having accession number (OP217064). BLASTn (https://blast.ncbi.nlm.nih.gov/Blast.cgi) was used to compare the *A. hystrix* COI gene with published COI sequences of related taxa from NCBI GenBank. Sequences of related taxa were aligned with *A. hystrix* COI gene sequence on the web version of Clustal Omega (https://www.ebi.ac.uk/Tools/msa/clustalo/). The aligned file was visualized and edited in BioEdit and used for the construction of the Maximum Likelihood (ML) phylogenetic tree on the IQ-TREE webserver (Nguyen et al., 2015). The analysis involved 15 representative sequences belonging to five *Atrina* species as the ingroup, and *Pinna bicolor* and *P. atropurpurea* as the outgroup terminal. The best-fitting substitution model using ModelFinder (Kalyaanamoorthy et al., 2017) was found to be Hasegawa-Kishino-Yano+F+G4 according to the BIC score. The robustness of the ML tree was analyzed by reiterating the observed data using an ultrafast bootstrap (Hoang et al., 2018) approximation for 5000 generations. The pairwise genetic distance between the species was determined by the Kimura 2-parameter method (Kimura, 1980) using MEGA X (Kumar et al., 2018). Shell specimen and tissues in 95% ethanol is stored in the Sathyabama Marine Museum, maintained in the Centre for Climate Change Studies, having voucher number: PS_AH_001.

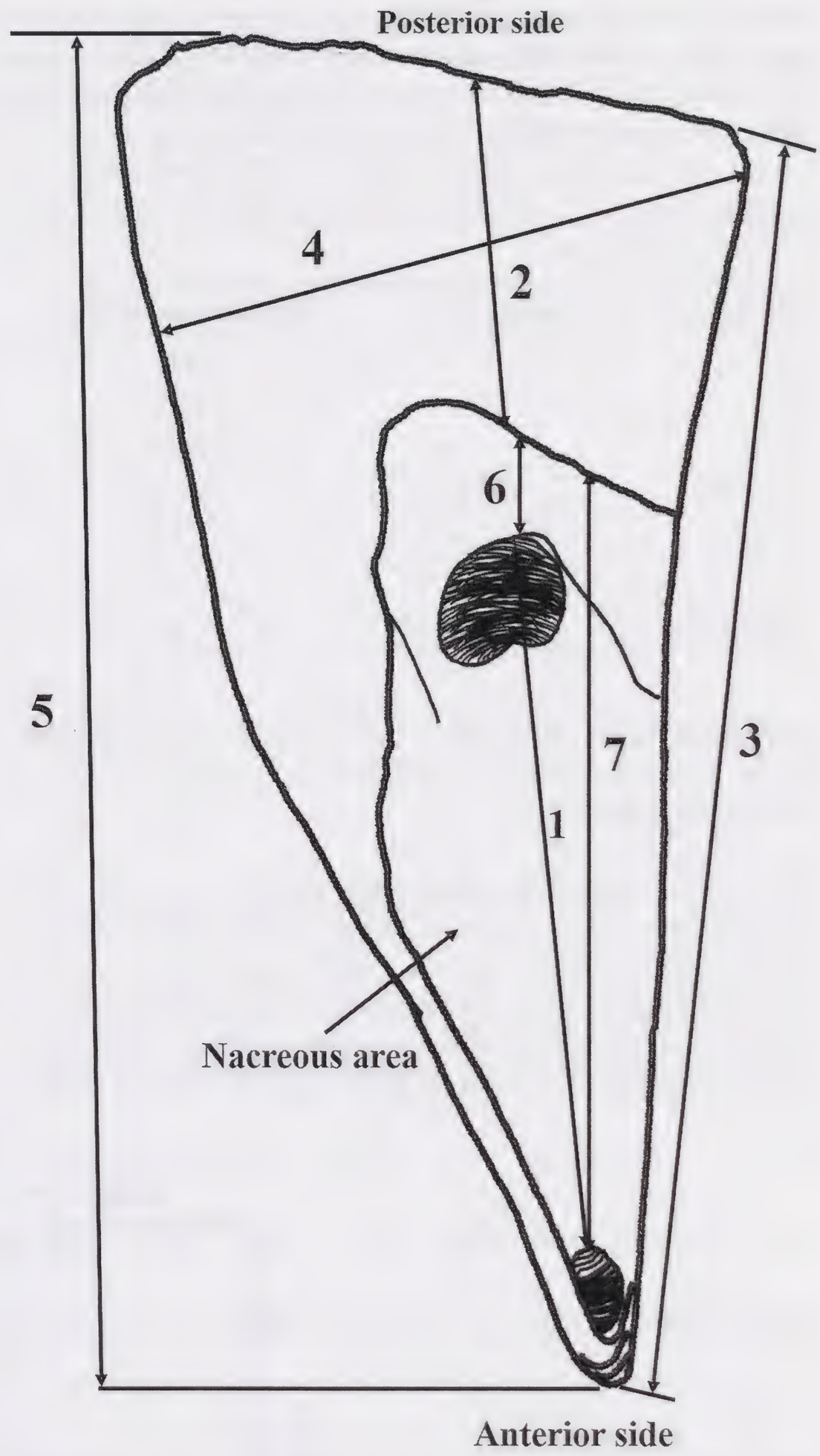

Figure 2. *Atrina hystrix*, shell diagram. 1. APAML = Anterior to Posterior Adductor Muscle Length; 2. PAMPSM = Posterior Adductor Muscle to Posterior Shell Margin; 3. DML = Dorsal Margin Length; 4. WL = Width; 5. TL = Total Length; 6. PAMPDNL = Posterior Adductor Muscle to Posterior Dorsal Nacreous Layer; 7. DNL = Dorsal Nacreous Length.

RESULTS

Phylum Mollusca
Class Bivalvia
Order Ostreida
Superfamily Pinnoidea Leach, 1819
Family Pinnidae Leach 1819

Genus *Atrina* Gray, 1842

Atrina hystrix (Hanley 1858)
(Figures 1, 2)

Atrina (Servatrina) hystrix (Hanley, 1858)

Description: Shell length and width to 15.8cm and 6.5cm respectively (Table 1). Shell width about three-quarters of total shell length. Roughly triangular, posterior margin flat. Valves usually fan-shaped, dorsal and ventral margins nearly equal in length. Color of shell internally and externally translucent, light-brown grading to dark brownish-purple toward the posterior side. Concentric sculpture consisting of fine growth lines convex posteriorly. About 15 narrow, radiating ribs present and preserved at anterior shell end. Ribs bearing regularly spaced fluted spines. Ventral margin posteriorly slightly convex and anteriorly concave. Dorsal margin usually straight, slightly shorter than ventral margin. Nacreous layer iridescent, occupying anterior part of internal valve surface. Posterior adductor muscle located 1.26 cm away from margin of the posterior dorsal nacreous layer. Posterior adductor muscle moderately large. Anterior adductor muscle small, located just anterior to tip of nacreous area. Sulcus absent, as in all *Atrina* species (Figures 1, 2).

Distribution: The distribution range of *A. hystrix* was limited to the Indo-West Pacific: Philippines (Lemer et al., 2014; Lemer et al., 2016), Indonesia, Thailand, and

Table 1. Measurements of the internal valve characters of *Atrina hystrix* collected in the present study; TL=Total Length; WL=Width; DML=Dorsal Margin Length; PAMPSM=Posterior Adductor Muscle to Posterior Shell Margin; APAML=Anterior to Posterior Adductor Muscle Length; DNL=Dorsal Nacreous Length; PAMPDNL=Posterior Adductor Muscle to Posterior Dorsal Nacreous Layer

Morphometric character	Measurement (cm)
TL	15.8
WL	6.5
DML	14.6
PAMPSM	3.80
APAML	8.12
DNL	9.77
PAMPDNL	1.26

New Caledonia (https://www.gbif.org/species/4592585). In the present study, we reported *A. hystrix* for the first time from India.

Molecular Identification and Phylogeny: BLASTn analysis revealed that the COI gene sequence was 98.2% similar to *A. hystrix* (with GenBank accession No. KJ366369). The phylogenetic analysis based on an ML tree constructed using a single mitochondrial gene fragment (COI – 657 nucleotide sites) resulted in a tree topology that *A. hystrix* from the present study is closely related to the same species previously reported in the Philippines (Lemer et al., 2014; Lemer et al., 2016). Out of 657 sites, 177 were parsimony-informative sites. In the ML tree, *A. hystrix* was sister to a clade comprised of *Atrina exusta* (Gmelin, 1791) and *A. vexillum*. Furthermore, *Atrina assimilis* (Reeve, 1858) formed a separate clade sister to the clade formed by *A. hystrix, A. exusta, and A. vexillum. Atrina pectinata* apparently diverged earlier in the evolutionary history of the group, forming a basal clade sister to all the other *Atrina* species in the tree. As expected, the genus *Atrina* and genus *Pinna* formed separate clades (Figure 3).

Additionally, the calculated pairwise genetic distance of COI gene fragment using the Kimura-2 parameter revealed a genetic distance of 0.021 or ~2% between *A. hystrix* of the present study and the existing sequence of *A. hystrix* in the NCBI GenBank. Additionally, *A. hystrix* showed around 21–29% genetic distance with congeners *A. vexillum*, *A. exusta, A. assimilis*, and *A. pectinata*. The genetic distance between *A. hystrix* and the *Pinna species, P. bicolor* and *P. atropurpurea,* was more than 35% (Table 2).

DISCUSSION

For the first time, we have reported pen shell *A. hystrix* from the Indian coast. Earlier the distribution of the species was limited to Indo-West Pacific (Lemer et al., 2014;

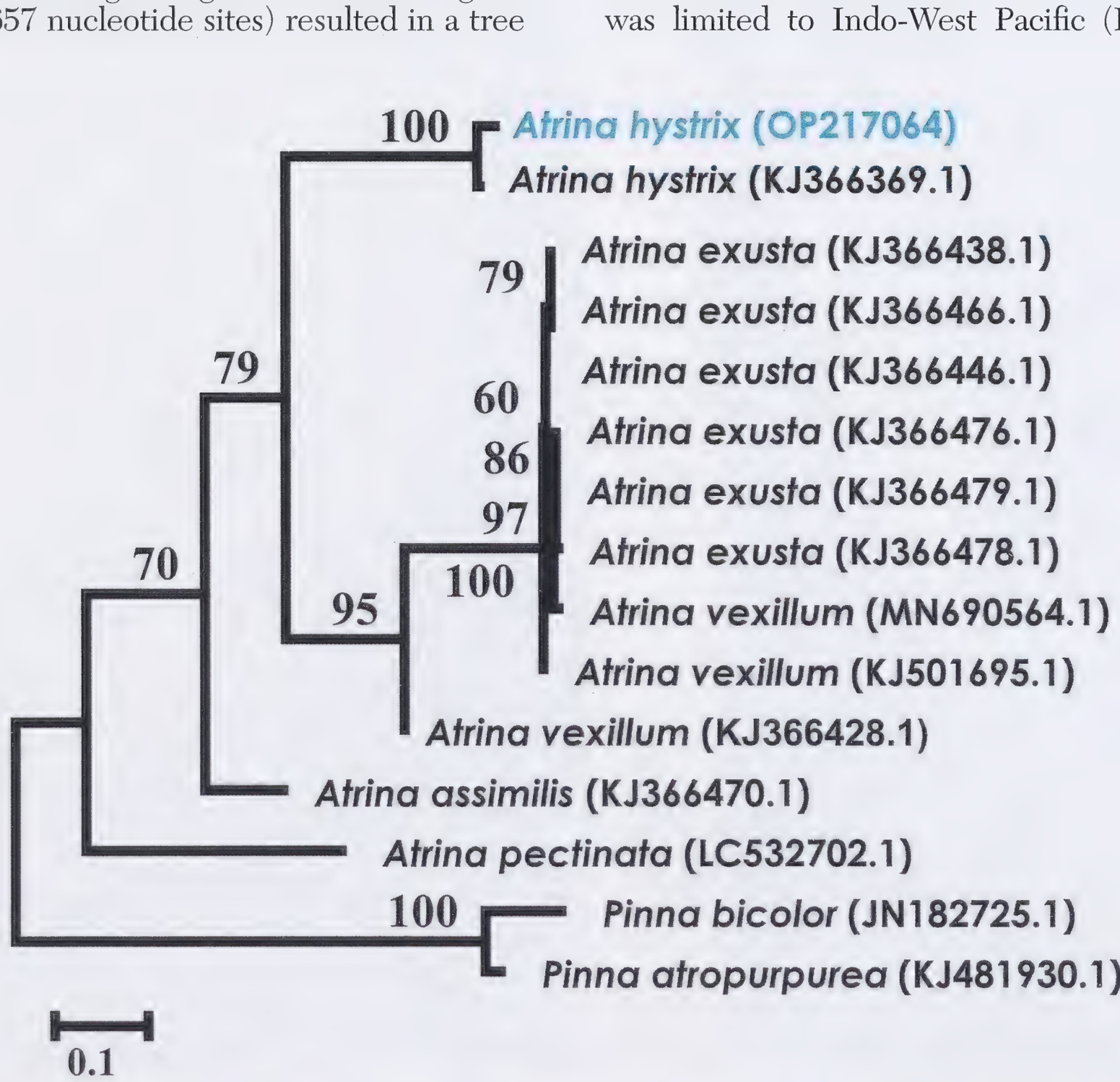

Figure 3. ML-based phylogenetic tree. Numbers near to the nodes show bootstrap support from 5000 bootstrap trees.

Table 2. Pairwise genetic distance between *A. hystrix* and other closely related taxa and outgroups. Analyses were conducted using the Kimura 2-parameter model. The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.4). This analysis involved 15 nucleotide sequences and a total of 657 positions in the final dataset.

Atrina hystrix (present study)													
Atrina hystrix (KJ366369.1)	0.021												
Atrina assimilis (KJ366470.1)	0.224	0.203											
Atrina exusta (KJ366478.1)	0.292	0.272	0.255										
Atrina exusta (KJ366438.1)	0.265	0.246	0.230	0.021									
Atrina exusta (KJ366446.1)	0.265	0.246	0.230	0.021	0.000								
Atrina exusta (KJ366466.1)	0.265	0.246	0.230	0.021	0.000	0.000							
Atrina exusta (KJ366476.1)	0.268	0.260	0.250	0.003	0.019	0.019	0.019						
Atrina exusta (KJ366479.1)	0.283	0.263	0.251	0.003	0.018	0.018	0.018	0.000					
Atrina vexillum (KJ366428.1)	0.213	0.190	0.206	0.149	0.133	0.133	0.133	0.134	0.142				
Atrina vexillum (MN690564.1)	0.291	0.271	0.259	0.011	0.020	0.020	0.020	0.008	0.008	0.147			
Atrina pectinata (LC532702.1)	0.257	0.259	0.246	0.281	0.251	0.251	0.251	0.270	0.276	0.236	0.268		
Atrina vexillum (KJ501695.1)	0.273	0.254	0.241	0.016	0.008	0.008	0.008	0.014	0.013	0.133	0.011	0.251	
Pinna bicolor (JN182725.1)	0.353	0.363	0.372	0.436	0.416	0.416	0.416	0.465	0.436	0.371	0.436	0.341	0.403
Pinna atropurpurea (KJ481930.1)	0.373	0.380	0.326	0.399	0.388	0.388	0.388	0.429	0.399	0.328	0.399	0.353	0.382	0.099

Lemer et al., 2016, https://www.gbif.org/species/4592585). Though the identity of *A. hystrix* is accepted, it is often confused with the closely related species *A. vexillum* and *A. pectinata,* due to the striking resemblance in their morphology and the phenotypic plasticity present within pinnid species (Rosewater, 1961). At one point, *A. hystrix* was regarded as a synonym of *A. vexillum* (Rosewater, 1961). However, closer morphological examination of specimens from the Indian Ocean revealed that *A. hystrix* is indeed a separate species (Lynge, 1909; Huber, 2010; Coan and Kabat, 2012). The exact position of the posterior adductor muscle scar with respect to the margins of the nacreous layer is one of the major (and few) taxonomic characters used to distinguish species of *Atrina* (Lemer et al., 2014). We agree with the separate identity of *A. hystrix* based on morphological comparison with *A. vexillum* and *A. pectinata*. In *A. vexillum*, the hind margin of the posterior adductor scar slightly protrudes beyond the nacreous area while in the collected specimen of *A. hystrix* (Poutiers, 1998), the posterior adductor muscle scar lies more than 1 cm below the posterior dorsal nacreous layer margin. Further, in *A. pectinata* the posterior adductor muscle scar lies 0.5–0.7 cm below the posterior dorsal nacreous layer margin which is shorter when compared to 1.26 cm in the current sample of *A. hystrix* (Poutiers, 1998). However, muscle scar characters should be used cautiously for identification of *A. pectinata* as it has been found to be a species complex (Liu et al., 2011; Lemer et al., 2014). The morphological examination revealing the identity of the present specimen as *A. hystrix* is further confirmed by molecular examination where we found the genetic divergence of less than 2% with previously reported *A. hystrix* from Philippines (Lemer et al., 2014), and clustering together in the phylogenetic tree with high bootstrap values.

CONCLUSION

For the first time, we have reported *A. hystrix* from India based on a morphological and molecular examination, making it fifth species of the genus *Atrina* in India.

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LITERATURE CITED

Balaji, S., J.K.P. Edward, and V.D. Samuel. 2012. Coastal and Marine Biodiversity of Gulf of Mannar, Southeastern India–A comprehensive updated species list. Gulf of Mannar Biosphere Reserve Trust, Publication 22: 128.

Coan, E.V. and A.R. Kabat. 2012. The malacological works and taxa of Sylvanus Hanley (1819–1899). Malacologia 55 (2): 285–359.

Folmer, O., M. Black, W. Hoech, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3 (5): 294–299.

Gmelin J.F. 1791. Vermes. In: Gmelin J.F. (Ed.) Caroli a Linnaei Systema Naturae per Regna Tria Naturae, Ed. 13. Tome 1(6). G.E. Beer, Lipsiae [Leipzig], pp. 3021–3910.

Gopalakrishnan, A., P.R. Divya, V.S. Basheer, T. Rajaswaminathan, A. Kathirvelpandian, K.K. Bineesh, R.G. Kumar, and J.K. Jena. 2012. Macro Flora & Fauna of the Gulf of Mannar a checklist: National Bureau of Fish Genetic Resources.

Gray, J.E. 1842. Molluscs. Pp. 48–92, in: Synopsis of the contents of the British Museum, edition 44. British Museum, London, iv + 308 p.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT.[London]: Information Retrieval Ltd., c1979–c2000. Paper read at Nucleic Acid Symposium Series.

Hanley, S. 1858. Description of new Pinnae. Proceedings of the Zoological Society of London.

Hoang, D.T., O. Chernomor, A. Von Haeseler, B.Q. Minh and L.S. Vinh. 2018. UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35 (2): 518–522.

Huber, M. 2010. Compendium of bivalves. Hackenheim, Germani. Conch Books.

Kalyaanamoorthy, S., B.Q. Minh, T.K.F. Wong, A.Von Haeseler and L.S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nature methods 14 (6): 587–589.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16 (2): 111–120.

Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35 (6): 1547.

Leach, W.E. 1819. Descriptions des nouvelles especes d'animaux decouvertes par la vaisseau Isabelle dans un boyage au pole boreal. Journal de Physique 88 (6):462–467.

Lemer, S., B. Buge, A. Bemis, and G. Giribet. 2014. First molecular phylogeny of the circumtropical bivalve family Pinnidae (Mollusca, Bivalvia): Evidence for high levels of cryptic species diversity. Molecular Phylogenetics and Evolution 75:11–23.

Lemer, S., D. Combosch, F. Sotto, G. Giribet, D. Dumale, and V. Soliman. 2016. The family Pinnidae (Bivalvia) in the Philippine archipelago: observations on its distribution and phylogeography. Nautilus 130 (4): 137–145.

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata [10th revised edition], vol. 1: 824 pp. Laurentius Salvius: Holmiae., available online at https://biodiversitylibrary.org/page/726886.

Liu, J., Q. Li, L. Kong, X. Zheng. 2011. Cryptic diversity in the pen shell *Atrina pectinata* (Bivalvia: Pinnidae): high divergence and hybridization revealed by molecular and morphological data. Molecular Ecology 20: 4332–4345.

Lynge, H. 1909. The Danish expedition to Siam 1899–1900. IV. Marine Lamellibranchiata. Kongliga Danske Videnskabernes Selskab, Selskabs Skrifter (Naturvidenskabelig og Mathematisk Afdelig), (ser.7), 5(3): 97–299 [also numbered 1–203], 5 pls., 1 map.

Martens, E.V. 1880. Mollusken. Pp. 179–353, pl. 19–22 In K. Möbius, F. Richters & E. von Martens, Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen. Berlin: Gutmann. available online at https://biodiversitylibrary.org/page/46619856.

Morton, B., R.S. Prezant, and B. Wilson. 1998. Class Bivalvia. Mollusca: The Southern Synthesis. Fauna of Australia. Vol 5. Part A xvi 563 pp, edited by P. L. Beesley, Ross, G.J.B. & Wells, A: CSIRO Publishing: Melbourne.

Nagabhushanam, A.K and G. Chandrasekhara Rao. 1972. An ecological survey of the marine fauna of Minicoy Atoll (Laccadive Archipelago, Arabian Sea). Mitteilungen aus dem Museum für Naturkunde in Berlin. Zoologisches Museum und Institut für Spezielle Zoologie (Berlin) 48 (2): 265–324.

Nguyen, L.-T., H.A. Schmidt, A.V. Haeseler, and B.Q. Minh. 2015. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32 (1): 268–274.

Poutiers, J.M. 1998. Bivalves (Acephala, Lamellibranchia, Pelecypoda). In: Carpenter, K. E. and V. H. Niem (eds.), FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 1. Seaweeds, corals, bivalves and gastropods. FAO, Rome, pp. 123–362.

Ramakrishna and A. Dey. 2010. Annotated Checklist of Indian Marine Molluscs (Cephalopoda, Bivalvia and Scaphopoda): Part-1. Records of Zoological Survey of India (Occasional) Paper (320): 1–357.

Ravinesh, R. and A Bijukumar. 2015. A checklist of the marine molluscs of Lakshadweep, India. Journal of Aquatic Biology & Fisheries 3:15–55.

Reeve, L. A. 1858–1859. Monograph of the genus *Pinna*. In: Conchologia Iconica, or, illustrations of the shells of molluscous animals, vol. 11, pl. 1–34.

Rosewater, J. 1961. The family PINNIDAE in the Indo-Pacific. Indo-Pacific Mollusca 1 (4): 175–226.

Rosewater, J. 1982. Review of Hawaiian Pinnidae and revalidation of *Pinna exquisita* Dall, Bartsch, and Rehder, 1938 (Bivalvia: Mytiloida).

Scheltema, A. 1983. *Pinna deltodes* Menke newly described and differentiated from *P. bicolor* Gmelin (Bivalvia, Pterioida). Journal of the Malacological Society of Australia 6 (1–2):37–52.

Schultz, P.W.W and M. Huber. 2013. Revision of the worldwide Recent Pinnidae and some remarks on fossil European Pinnidae: ConchBooks.

Stella, C., P. Paul, and C. Ragunathan. 2015. Three New distributional records of Pen Shells (Bivalvia: Pinnidae) from Seagrass beds of Palk Bay Area in Tamil Nadu. Sustainability, Agri, Food and Environmental Research 3 (1).

Turner, R.D. and J. Rosewater. 1958. The family Pinnidae in the western Atlantic. Johnsonia 3 (38): 285–326.

Vaitheeswaran, T. and S. Malathi. 2015. A new lamellated pen shell *Atrina lamellata* habe, 1961 (Family: Pinnidae) (Barnes, 1987) off Thoothukudi coast of Gulf of Mannar, India (08° 35′22.5″ N, 78° 27′40.9″ E)–(310 m). International Journal of Fish Aquatic Studies 2015e 2 (5): 55–56.

Expansion of *Crepidula fornicata* (Linnaeus, 1758) (Gastropoda: Calyptraeidae) in the North Sea drives the species into new niches

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ABSTRACT

Crepidula fornicata (Linnaeus, 1758) is continuing its expansion along the Dutch coast. Although the species is a generalist that occupies a wide range of substratum types, recent observations from the coast of Zuid-Holland (The Netherlands) show it continues to occupy new niches, from which it has not been recorded elsewhere. The species has been found on the inside of hermit crab-occupied gastropod shells. More recently it has adapted to living on various species of infaunal bivalve shells.

Additional Keywords: Introduced species, invasive species, invasion success

INTRODUCTION

As summarized in Raven (2019), in the late 19th century, the Common Atlantic Slipper Snail *Crepidula fornicata* (Linnaeus, 1758) reached the United Kingdom from the east coast of North America and spread throughout the North Sea, with first records from the Netherlands in 1929. There it became abundant in the delta and in the Wadden Sea, where they mainly grow on oysters and mussels (De Bruyne *et al.*, 2013). The sandy seabed of the province Zuid Holland did not provide sufficient suitable substrate, and the species was always found attached to shells: the outside of mussels *Mytilus edulis* Linnaeus, 1758, the inside or outside of dead bivalves, and on the outside of hermit crab-occupied shells of *Buccinum undatum* (Linnaeus, 1758).

To protect the coast during storms, replenishment with large volumes of sand starting in the mid-1970s gradually changed the coastal profile, and the local fauna (Raven, 2020). During the last decade, *Euspira catena* (Da Costa, 1778) particularly benefitted. After storms in the winters from 2017 to 2022 hundreds of living specimens and fresh-dead shells occupied by hermit crabs washed up on the shore. The latter frequently had multiple specimens of *Crepidula fornicata* on the outside, some of them forming stacks. In 2017, the first specimens were observed with *C. fornicata* living on the inside, taking a very flat shape apparently not hindered by the movements of the hermit crabs (Raven, 2019), a niche not occupied before by this species in the North Sea area. In 2021, the first living infaunal bivalve, *Spisula subtruncata* (da Costa, 1778), with a slipper shell attached was found (Raven, 2021), quickly followed by additional specimens, on other species of infaunal bivalves (Raven and Verheijen, 2021; this paper) – a niche not occupied elsewhere by this species. Specimens were also seen on rocks and loose pieces of wood. Likely, they already occupied the latter niches, but it illustrates the flexibility of this species in occupying new niches.

MATERIALS AND METHODS

This work is based on the visual inspection of washed-up material by five persons through regularly walking several kilometers along the beach at various localities during 2021 and 2022, mostly along the coast of the province Zuid-Holland, The Netherlands (Figure 1). The largest number of invertebrates was invariably observed after storms, but several specimens were found during calm periods. These observations are put into perspective based on five decades of observations along this coast by the author.

RESULTS

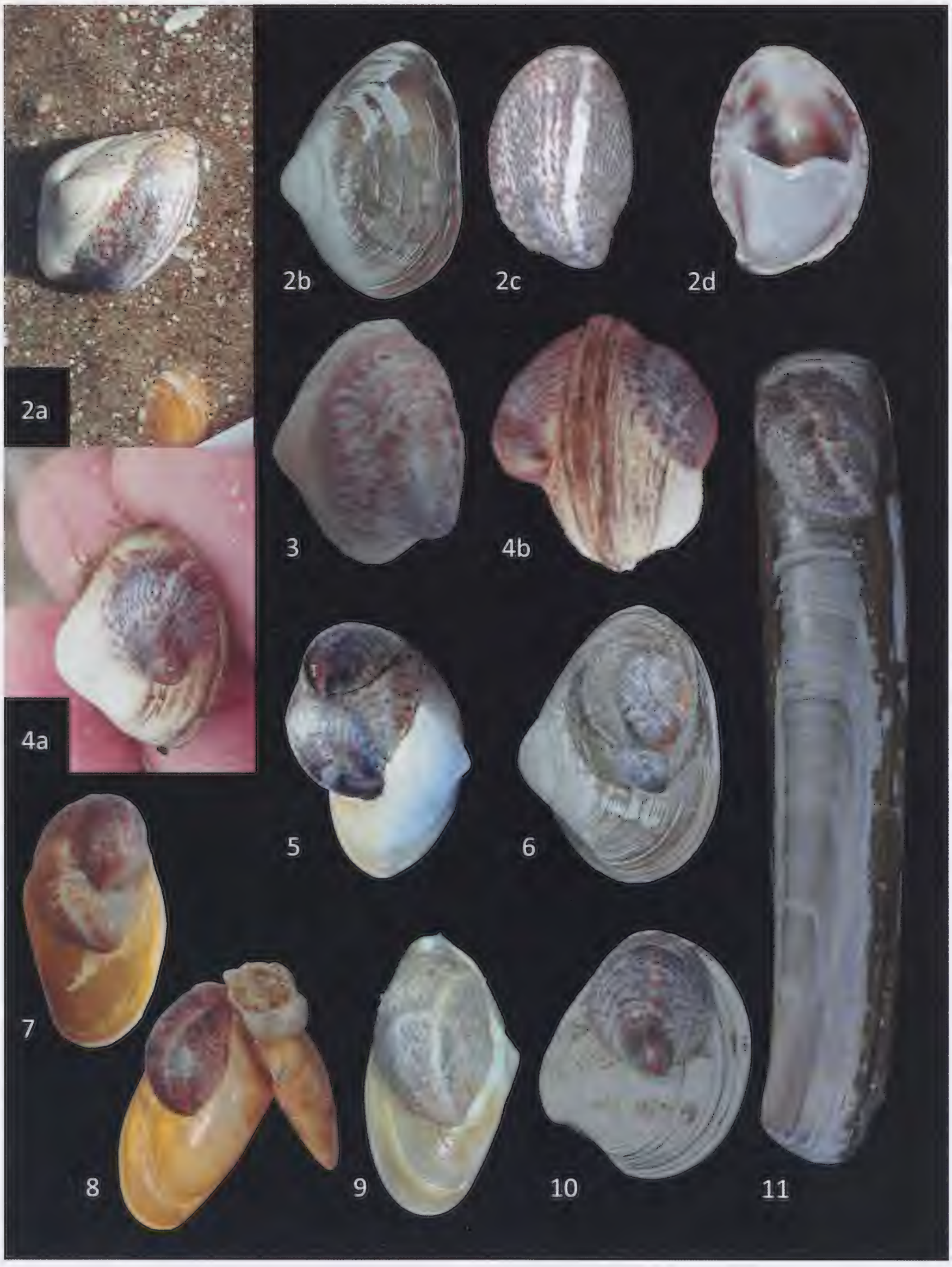
After the storm of 5–6 April 2021, the beaches along the coast of Zuid-Holland were covered by dead and dying invertebrates, representing the fauna of a substantial part of the nearby seabed. This included an estimated hundreds of thousands of specimens of the bivalve *Spisula subtruncata* (da Costa, 1778). On 7 April 2021, on the Noorderstrand, Scheveningen, The Hague (Figure 1) the author found a single living specimen of that bivalve with a *C. fornicata* attached as epibiont (Figure 2). This is remarkable, as the bivalve lives buried in sand. That the slipper snail lived on the bivalve whilst it was buried in the sediment is demonstrated by the position of the epibiont: attached to the left valve, with its head towards the posterior end of the bivalve where the siphons are located. As the bivalve has very short siphons, the head of the suspension feeding slipper snail would be at the sediment

Figure 1. Study location map. Modified from Google Maps.

surface with a water flow created by the siphons, allowing it to breathe and eat. As both animals grew, the slipper snail must have gradually displaced itself to keep its head in the same position. As always, the slipper snail adapted its shape to its host. Underneath the shell the periostracum of the bivalve was preserved and the outline of the shell, and within that the outline of the foot of the slipper snail are clearly visible (Figure 2b). These marks allow correct repositioning of the slipper snail(s) on their host shells after cleaning.

After a mention of this find in the Facebook group of the Netherlands Malacological Society, another find with similar characteristics (Figure 3) was recorded on 24th May 2021 by Jan Adema, this one from the North Sea beach at Ameland Island, north of the Wadden Sea (Figure 1). In this case, the host died some time before it was washed up, as can be seen from the bryozoans on the inside of the valve. The slipper snail likely started its life as the specimen above, but after the death of its host it could continue to live as the bivalve was washed out of the sediment, as is shown by the bryozoans on the inside of the valve. Both finds were published (Raven, 2021). In that paper the situation was compared to that of barnacles that around the same time had been found frequently on the posterior area of other infaunal bivalves, *Donax vittatus* (da Costa, 1778) (Figure 12) and *Ensis leei* Huber, 2015.

During August and October 2021, Frank Wesselingh (Naturalis) and Marco Verheijen (Noordwijkerhout) found additional specimens in the Katwijk-Noordwijkerhout area, further north along the coast of Zuid-Holland (Raven and Verheijen, 2021; see Table 1 for an overview of all specimens found). This included a *Spisula subtruncata* with a slipper snail on each valve (Figure 4) and one with a stack of two slipper snails (Figure 5), as well as a *Donax*



Figures 2–11. *Crepidula fornicata* and host mollusks. **2–6.** On *Spisula subtruncata*. **2.** Northern beach at Scheveningen, 12.iv.2021, leg. J.G.M. Raven (R 02130), *C. fornicata*, L = 24.5 mm; *S. subtruncata*, L = 28.4 mm. **2a.** On the beach. **2b.** Valve with slipper snail removed, showing scars. **2c, d.** *Crepidula fornicata*. **3.** On a valve of *Spisula subtruncata*, Ameland, 24.v.2021, leg. J. Adema. **4.** Two individuals on a living *Spisula subtruncata* with algae in the siphonal region, Noordwijkerhout, 22.viii.2021, leg. F. Wesselingh, *S. subtruncata* L ~2.5 cm. **4a.** On the beach. **4b.** Ventral view showing two slipper snails. **5.** Stack of two individuals on a valve, Duindamse Slag, Noordwijk, 5.x.2021, leg. M. Verheijen, *S. subtruncata* L 23 mm. **6.** Stack of four individuals on a living *S. subtruncata* that also has the scars of two barnacles on siphonal area, Katwijk northern beach, 17.i.2022, leg. G. Mulder (GM 13060d); largest *C. fornicata*, L = 22.5 mm; *S. subtruncata*, L = 32.7 mm. **7–11.** *Crepidula fornicata* on other bivalves. **7.** Stack of two inidviduals on a living *Donax vittatus*, Duindamse Slag, Noordwijk, 9.x.2021, leg. M. Verheijen; *C. fornicata*, L = 19 mm; *D. vittatus*, L = 30 mm. **8.** Single individual and a barnacle on a living *D. vittatus*, Duindamse Slag, Noordwijk, 9.x.2021, leg. M. Verheijen; *C. fornicata*, L = 17 mm; *D. vittatus*, L = 30 mm. **9.** On a living *Donax vittatus*, Katwijk northern beach, 17.i.2022, leg. G. Mulder (GM 13060g); *C. fornicata*, L = 21.0 mm; *D. vittatus*, L = 27.3 mm. **10.** On a living *Chamelea striatula*, Katwijk northern beach, 17.i.2022, leg. G. Mulder (GM 13060h); *Crepidula fornicata*, L = 18.6 mm; *Chamelea striatula*, L = 29.1 mm. **11.** On a living *Ensis leei*, Langevelderslag, Noordwijk, 23.xii.2021, leg. G. Mulder (GM 04662); *C. fornicata*, L = 22.9 mm; *E. leei*, L = 11.5 cm.

Table 1. Overview of all infaunal bivalves recorded with *Crepidula fornicata*.

Host		# specimens *Crepidula*		Locality	Date	Observer
Name	**Length (mm)**	**Right valve**	**Left valve**			
Spisula subtruncata	28.4	1	0	Scheveningen (north)	7.iv.2021	Han Raven
Spisula subtruncata	~30	1	absent	Ameland	24.v.2021	Jan Adema
Spisula subtruncata	23	2	absent	Noordwijk	5.viii.2021	Marco Verheijen
Spisula subtruncata	25	1	1	Noordwijkerhout	22.viii.2021	Frank Wesselingh
Donax vittatus	30	absent	2 barnacle	Noordwijk	9.x.2021	Marco Verheijen
Ensis leei	115	1	0	Noordwijk (Langevelderslag)	23.xii.2021	Gab Mulder
Spisula subtruncata	32.7	0, barnacle scar	4; barnacle scar	Katwijk (north)	17.i.2022	Gab Mulder
Spisula subtruncata	25.5	absent	2	Katwijk (north)	17.i.2022	Gab Mulder
Spisula subtruncata	29.8	0	1	Katwijk (north)	17.i.2022	Gab Mulder
Spisula subtruncata	28	0	2, with living barnacles*	Katwijk (north)	17.i.2022	Gab Mulder
Donax vittatus	27.3	0	1	Katwijk (north)	17.i.2022	Gab Mulder
Chamelea striatula	29.1	1	0	Katwijk (north)	17.i.2022	Gab Mulder

* barnacle scars inside demonstrate specimen was long dead

vittatus with a slipper snail on one valve and a barnacle on the other (Figure 8), and a specimen of the same species with a stack of two slipper snails (Figure 7).

Despite various additional visits to various beaches of The Hague throughout the year, no further specimens were found. However, in December 2021 and January 2022, Gab Mulder (Naturalis) made numerous visits to the beaches between Hoek van Holland and Noordwijk (Figure 1) during two of which he found a substantial number of other specimens (Table 1), not only of slipper snails on the two bivalve species mentioned above (Figure 9), but also on *Chamelea striatula* (da Costa, 1778) (Figure 10) and on *Ensis leei* Huber, 2015 (Figure 11). The latter is remarkable because, although it has short siphons, it can withdraw deeper below the sediment surface. Overall, the large majority of specimens was found in the area Katwijk-Noordwijkerhout, but that is also the stretch of coast that has been visited most frequently.

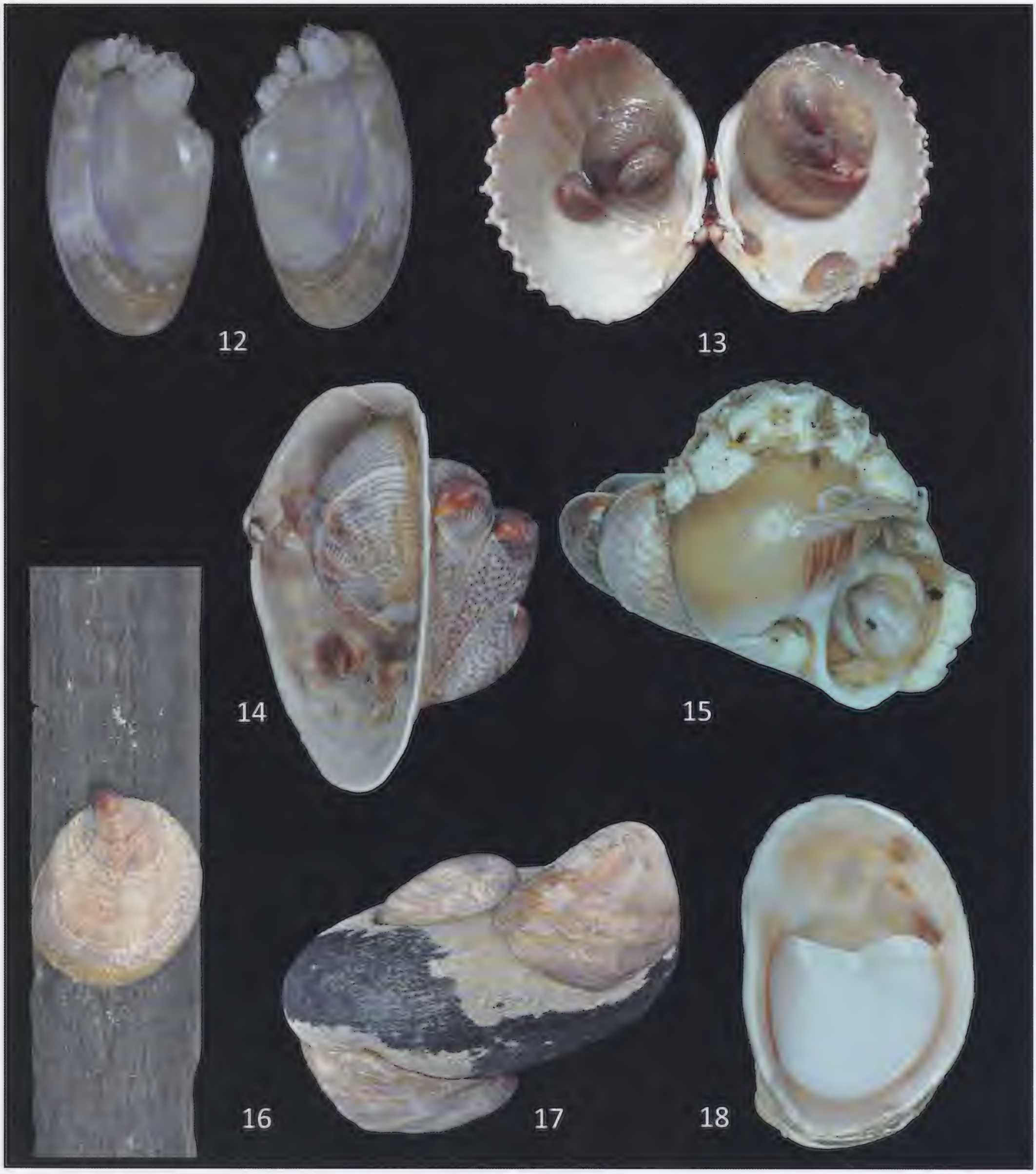
DISCUSSION

All the bivalves involved are shallow burrowers with very short siphons, and the slipper snails are all located on the outside at the posterior extremity of the bivalves, with their heads close to the siphonal area. This is evidence that the slipper snails lived on bivalves while these latter were living within the sediment, not on specimens that were located at the sediment surface, in which case they would be positioned at random positions on the bivalves.

For several individuals found on an empty valve of *Acanthocardia echinata* (Linnaeus, 1758) from Hoek van Holland (Figure 13), orientation of the largest snails suggests the shell became occupied when still in the sediment, therefore the snails have their mouths towards the opening and surface. Otherwise, the valves would already have been separated, as the ligament is not very strong (Raven, 2019).

As Raven (2021) previously mentioned, the occurrence of slipper snails on infaunal bivalves is not unique. The shells of many shallow-burrowing bivalves are used as substratum by epibionts, as it had been described for slipper snails (Peterson, 1983), but thus far this had not been recorded for *Crepidula fornicata*. Peterson (1983) collected *Chione undatella* (G.B. Sowerby I, 1835) and *Protothaca staminea* (Conrad, 1837) from a seagrass field in California, and found *Crepidula onyx* G.B. Sowerby I, 1824 on ~1% of the first and none of the latter. Those collected bivalves were observed during the following two years and slipper snails continued to settle on *Chione undatella*, more than 100 times more frequently on already occupied hosts, whilst none settled on *Protothaca staminea*. Peterson (1983) attributes this preference for *Chione* to its shorter siphons, which means it has to stay close to the sediment surface, just as seen in the four species on which slipper snails have thus far been recorded in the Netherlands. Peterson also noted the specimens hosting slipper snails grew slower than those without epibionts, which he interpreted as due to competition for food.

Thieltges *et al*. (2003: table 3) observed *Crepidula fornicata* on a very small percentage of the cockle *Cerastoderma edule* (Linnaeus, 1758) living in mussel beds and tidal flats of the German Wadden Sea. *Cerastoderma edule* is an infaunal bivalve, but regrettably no details were provided in the paper. Dr Thieltges (pers. comm.) explained that the slipper snails occurred only on exposed cockles entangled in the byssus of mussels from mussel beds or on cockles that were only half buried



Figures 12–18. *Crepidula fornicata* and other epibionts mentioned in this study. **12.** Barnacles on a living *Donax vittatus*, Scheveningen, 10.ii.2021, leg. J.G.M. Raven, L 28.8 mm (from Raven, 2021: fig. 9). **13.** On an empty valve of *Acanthocardia echinata*. Strong, Hoek van Holland, ii.2019, leg. J.G.M. Raven, L 40 mm (from Raven, 2019: fig. 4). **14.** A stack of three slipper snails on the outside, a stack of two and three juveniles on the inside of a valve of *Mya truncata* Linnaeus, 1758, also partially overgrown by bryozoans. Largest and oldest *C. fornicata*, L = 29.2 mm); large individuals on the inside have their mouths toward the posterior end, Hoek van Holland, 2.ii.2022, leg. G. Mulder (GM 13078a), L 41.2 mm. **15.** Slipper snails on the outside and within the aperture of a *Euspira catena* (da Costa, 1778) that was occupied by a hermit crab, Scheveningen northern beach, i.2017, leg. J.G.M. Raven, H ~35 mm (from Raven, 2019: fig. 5). **16.** On a piece of wood (only the central part is shown) that also has several shipworm boreholes (*Teredo navalis* (Linnaeus, 1758)); *C. fornicata*, L = 37.9 mm; wood, L = 28.4 cm, Hoek van Holland, 2.ii.2022, leg. G. Mulder (GM 13078d). **17.** Three specimens on a coal pebble with bryozoans; the byozoan crust continues underneath the snails; largest *C. fornicata*, L = 33.2 mm; pebble, L = 5.9 cm, Katwijk northern beach, 17.i.2022, leg. G. Mulder (GM 13060c). **18.** Large specimen of *C. fornicata* (L 6.5 cm) from the calm waters of the harbor at Burghsluis, Zeeland, 17.x.2003, leg. G. Mulder (GM 04191).

in the sediment (due to whatever reason), never on fully buried cockles. And only single individuals, never stacks. This is therefore not comparable to the situation along the Dutch coast.

Along the Zuid-Holland coast, the larvae that settle on empty bivalves have a strong preference for those shells that are already occupied, settling either on other slipper limpets or directly on the valve (Figures 13–14; Raven, 2019: fig. 4). However, the larvae more frequently select hermit crab-occupied gastropods (Figure 15; Raven, 2019: figs 2–3, 5–10), on which numerous individual specimens may settle (at least up to 16, Raven, 2019: table 2) and long stacks may form (Raven, 2019: fig. 3). Thieltges (2003: fig. 3) shows a more extreme example form the German Wadden Sea, with a large area covered by such stacks. The stacks are key to their reproduction as the oldest and largest specimens are female, the younger and smaller male, with those in between being protandrous hermaphrodites (e.g., Fretter and Graham, 1981; Collin, 2006). This means that the planktic larvae of slipper snails can locate other specimens of their species. In infaunal bivalves, their choice is much more limited, as they can only opt to settle either on top of the first occupant, or on the other valve. The infaunal bivalves along the coast of Zuid-Holland usually have one or two snails on their shells, as individuals or a short stack. A single specimen was found with a stack of four snails (Figure 6), which must have strongly affected the burrowing capacity of the host. Generally, the snails will survive the death of their host, as empty shells on the seabed are also frequently colonized (Figure 14) and the snails are then less restricted in growth, but of course stand a higher risk of being washed up on the beach as they no longer have a host that anchors them within the sediment.

Gordillo and Archuby (2014) studied a Pleistocene deposit in Patagonia. The venerid *Ameghinomya antiqua* (P.P. King, 1832), a species with short siphons, could live completely buried in the sediment, but often shows a semi-infaunal orientation, with the umbonal region of the shell above the sediment-water interface. Such specimens had apparently been colonized by *Crepidula* species–recognizable by the marks of foot and outline they left on their host shells (Gordillo and Archuby, 2014: fig. 4). These are very similar to the marks shown on Figure 2b herein (even more detail is visible on Raven, 2019: fig. 16). Gordillo and Archuby found that many of the bivalves studied had drill holes of the carnivorous muricid *Trophon geversianus* (Pallas, 1774), which had a clear preference for the umbonal area of the valves. On the other hand, only four out of 53 specimens with marks of slipper snails had drill holes, suggesting the slipper snails prevented the host from being attacked by drilling predators. The authors therefore called this a "symbiosis", even though they also noted that bivalves with slipper snails likely were less able to dig themselves in, making them more vulnerable to attacks by other predators, especially crabs.

Similarly, the infaunal bivalves along the coast of Zuid-Holland may be less able to dig themselves in properly. Although that could render them more vulnerable to predation by crabs, the slipper snails also substantially increase the area of the exposed surface, thus making such attacks harder. So far there is no evidence of such crab attacks on living infaunal bivalves with slipper snails. On the other hand, Peterson (1983) concluded that slipper snails living on infaunal bivalves are themselves less vulnerable to crab attacks than snails living on epifaunal substrates.

The presence of slipper snails does not protect infaunal bivalves against attacks by another key predator that is very abundant in the study area–the naticid *Euspira catena*, as it leaves the umbonal area uncovered. *Euspira catena* does not attack above the sediment surface as muricids do, but lives in the sand and generally drills a hole close to the umbo of infaunal bivalves. This is demonstrated by the fresh bivalve shells (mostly *Spisula subtruncata*) that the author collected from San Lorenzo beach (Asturias, Spain), many of which have drill holes, all tapering as is characteristic for naticids (Smith, 2022). At that locality, the only naticid that is large enough to produce that size of holes is *Euspira catena*. The large majority of drill holes is located near the umbo, and the author has observed the same at numerous other localities on a range of species of infaunal bivalves, including along the coast of Zuid-Holland. No infaunal bivalves with slipper shells have been found that were attacked by naticids, but thus far only a small number of occupied bivalves have been recorded.

As mentioned above, in the Netherlands, *Crepidula fornicata* has been observed to occupy a wide range of substratum types. In recent years, not only the number of slipper snails washing up on the coast of Zuid-Holland has apparently markedly increased, but also the variety in objects on which they live. There, by far most slipper snails are found on naticids inhabited by hermit crabs, with smaller numbers on living mussels, empty shells, hermit crab-occupied whelks, large stones, wood, and other objects (Figures 13–17). Elsewhere in the Netherlands they have (among others) also been recorded living on the free-swimming *Aequipecten opercularis* (Linnaeus, 1758), on which the snail formed ridges reflecting the ribs of the bivalve on which it lived (Doeksen and Peeters, 2020).

Raven (2019) concludes that the success in reproduction is the driving force behind its adaptation to new niches. The remarkable and most recently observed adaptations are living inside hermit crab-occupied gastropod shells (first recorded January, 2017–see Raven, 2019) and more recently attaching to the shells of infaunal bivalves (first recorded April 2021–see Raven, 2021). The first is rare in its original range and new for the North Sea (Raven, 2021), the latter new for its entire range, and therefore appear to be behavioral shifts.

Although most records of slipper snails living on infaunal bivalves are from *Spisula subtruncata*, the number of host species from which they are recorded is

increasing. The number of observations on this phenomenon is also quickly increasing, but that may be in part due to the increased awareness of beachcombers and other observers regarding epibionts. Various beachcombers told the author they recently observed slipper shells on infaunal bivalves, but did not collect or record them. Although the number of infaunal bivalves with slipper snails as epibionts is currently low (a few occurrences among an estimated hundreds of thousands bivalves washed up on beaches) it may further expand to species such as *Cerastoderma edule*, *Spisula solida* (Linnaeus, 1758), *Mactra corallina* (Linnaeus, 1758), *Venerupis corrugata* (Gmelin, 1791) and *Ruditapes philippinarum* (A. Adams and Reeve, 1850), which wash up in much smaller numbers. Deeper-burrowing species with longer siphons such as *Lutraria lutraria* (Linnaeus, 1758) and *Mya truncata* Linnaeus, 1758 are not suitable as hosts. Interestingly, although only indirect evidence is at hand–from the fauna washed up on beaches following storms–the density of slipper snails along the coast of Zuid-Holland is apparently much lower than observed in the German parts of the Wadden Sea, where Thieltges (2003) observed entire areas covered with stacks of these animals, at least hundreds per square meter. Further expansion therefore appears feasible.

Parker *et al.* (2013) state that the fundamental assumption in invasive biology, that most invasive species exhibit enhanced performance in their introduced range relative to their home range, has led to numerous hypotheses explaining "invasion success" by altered ecological and evolutionary pressures. They found that some invasive species perform better in their new ranges, but just as many perform similarly across ranges. The increase in suitable substrates (especially hermit crab-occupied naticid shells) led to an enormous increase in the number of slipper snails along the coast of Zuid-Holland, which led to the adaptation to new niches. This has thus far only been observed in the North Sea where *Crepidula fornicata* has been introduced. Therefore, in this case the hypothesis of "invasion success" leading to altered ecological and evolutionary pressures appears to be confirmed. In favorable habitats they can also become very large, such as the specimens living on wooden poles in the quiet waters of the harbor of Burghsluis (Zeeland, The Netherlands; Figure 18). Their length of 6.5 cm is well above the length of 2–5 cm recorded in its original range (Abbott, 1974).

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LITERATURE CITED

Abbott, R.T. 1974. American Seashells (2nd edition). Van Nostrand Reinhold, New York.

De Bruyne, R.H., S. van Leeuwen, A. Gmelig-Meyling, and R. Daan (eds.). 2013. Schelpdieren van het Nederlandse Noordzeegebied. Ecologische atlas van de mariene weekdieren (Mollusca). Tirion Natuur en Stichting ANEMOON, Leiden.

Collin, R. 2006. Sex ratio, life-history invariants, and patterns of sex change in a family of protandrous gastropods. Evolution 60(4): 735–745.

Doeksen, G. and K. Peeters. 2020. Muiltjes (*Crepidula fornicata*) met aangepaste sculptuur op wijde mantelschelpen (*Aequipecten opercularis*). Het Zeepaard 80(4): 166–168.

Fretter, V. and A. Graham. 1981. The prosobranch molluscs of Britain and Denmark. Part 6. Journal of Molluscan Studies, Supplement 9: 309–313.

Gordillo, S. and F. Archuby. 2014. Live-live and live-dead interactions in marine death assemblages: The case of the Patagonian clam *Venus antiqua*. Acta Palaeontologica Polonica 59(2): 429–442.

Parker, J.D., M.E. Torchin, R.A. Hufbauer, N.P. Lemoine, C. Alba, D.M. Blumenthal, O. Bossdorf, J.E. Byers, A.M. Dunn, R.W. Heckman, M. Hejda, V. Jarošik, A.R. Kanarek, L.B. Martin, S.E. Perkins, P. Pyšek, K. Schierenbeck, C. Schloder, R. van Klinken, K.J. Vaughn, W. Williams, and L.M. Wolfe. 2013. Do invasive species perform better in their new ranges? Ecology 94: 985–994

Peterson, C.H. 1983. Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* Sowerby and *Cancer anthonyi* (Rathbun). Journal of Experimental Marine Biology and Ecology 68(2): 145–158.

Raven, J.G.M. 2017. Mooie vondsten na de storm van 13 januari 2017 en reflecties op veranderingen in de kustfauna van Zuid-Holland. Spirula 411: 27–34.

Raven, J.G.M. 2019. *Crepidula fornicata* (Linnaeus, 1758) as hermit crab commensal in the North Sea. The Nautilus 133(2): 1–8.

Raven, J.G.M. 2020. Mollusken van zandopspuitingen op het Noorderstrand (Scheveningen, Zuid-Holland). Spirula 423: 12–28.

Raven, J.G.M. 2021. Een Muiltje *Crepidula fornicata* (Linnaeus, 1758) levend op een ingegraven tweekleppige). Spirula 428: 13–15.

Raven, J.G.M. and M. Verheijen. 2021. Meer Muiltjes *Crepidula fornicata* (Linnaeus, 1758) op ingegraven levende tweekleppigen. Spirula 429: 22–23.

Smith, J. 2022. Drilling Predation in the Fossil Record. In: Digital Atlas of Ancient Life. Paleontological Research Institution, Paleontological Research Institution https://www.digitalatlasofancientlife.org/learn/paleoecology/predation/drilling-predation/ (consulted 30 October 2022.)

Thieltges, D.W. 2003. Erfolgreiche Einwanderin aus Übersee – Die Amerikanische Pantoffelschnecke *Crepidula fornicata* im Wattenmeer. Natur und Museum 133(4): 110–114.

Thieltges, D.W., M. Strasser and K. Reise. 2002. The American slipper limpet *Crepidula fornicata* (L.) in the northern Wadden Sea 70 years after its introduction. Helgoland Marine Research (2003) 57: 27–33.

First record of *Aphelodoris antillensis* Bergh, 1879 (Gastropoda: Nudibranchia) from the southwestern Atlantic Ocean

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ABSTRACT

The nudibranch *Aphelodoris antillensis* Bergh, 1879 was originally described from St. Thomas, Virgin Islands, and later recorded from Bermuda, Florida, and across the entire Caribbean region south to Colombia and Venezuela. This paper reports the first record of *A. antillensis* from the southwestern Atlantic Ocean, as a result of the collection of one specimen from Brazil. The specimen presents the characteristic translucent-white mantle scattered with small reddish-brown spots, a large, granular prostate, and a very close connection between the uterine duct and the vagina with the bursa copulatrix. The present record expands the known geographic distribution of *A. antillensis* more than 6,000 kilometres southward.

Additional Keywords: Gastropoda; Heterobranchia, Doridina, Dorididae, SEM

INTRODUCTION

The genus *Aphelodoris* was introduced by Bergh (1879) and is characterized by a smooth mantle, anterior border of the foot notched, grooved oral tentacles, radula with unicuspid hook-shaped teeth, absence of rachidian teeth, and a triaulic reproductive system with a large granular prostate (Valdés, 2002). *Aphelodoris* is distributed along the Indo-Pacific region and the Caribbean Sea (Wilson, 2003) including ten valid species (MolluscaBase, 2022). *Aphelodoris antillensis* Bergh, 1879, the type species of the genus, is translucent-white with a variable amount of dark-red or brown pigment on the mantle, reaching up to 30 mm in length (Hamann, 1992). This species was originally described from St. Thomas, Virgin Islands (Bergh, 1879) and later recorded from Bermuda (Verrill, 1900, as *Doris* (?) *bistellata*), Florida (Ev. Marcus and Er. Marcus, 1967), and across the entire Caribbean region as south as Colombia and Venezuela (Hamann, 1992; Quiroga *et al.*, 2004; Valdés *et al.*, 2006).

Many nudibranch species with a wide geographic distribution in the Caribbean Sea (e.g., *Cadlina rumia* Marcus, 1955 and *Flabellina engeli* Ev. Marcus and Er. Marcus, 1968) were also recorded in different regions of the Brazilian coast (Ev. Marcus, 1977; Padula and Santos, 2006; Padula et al. 2012). The diversity of nudibranch species in the tropical and subtropical western Atlantic has been the subject of several studies along the recent years. Recent reports of new records and descriptions of new species indicate that many species remain potentially undiscovered in the region (Alvim and Pimenta, 2013; Jörger *et al.*, 2014; Padula *et al.*, 2012, 2014; Galvão Filho *et al.*, 2015; Lima and Simone, 2018; Cetra and Roche, 2019). The present paper reports the first record of *Aphelodoris antillensis* from the southwestern Atlantic as a result of collection of one specimen from Brazil. Detailed information of color of the living specimen, external and internal morphology is provided and discussed.

MATERIALS AND METHODS

A single specimen was collected by hand under a rock while scuba diving at Ilha da Âncora, Armação dos Búzios, Rio de Janeiro State, southeastern Brazil (22°46′10″ S, 41°47′20″ W). The specimen was photographed alive, measured, preserved in 70% ethanol and deposited

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in the malacological collection of the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Brazil. Informative taxonomic characters of the external and internal morphology were observed under a stereomicroscope. The specimen was dissected, the buccal bulb extracted, the radula and jaw were cleaned in a solution of sodium hydroxide to dissolve surrounding tissue and later rinsed in water. The radula and jaw were subsequently placed on a stub for scanning electron microscope (SEM) examination at Plataforma de Microscopia Eletrônica Rudolf Barth, Fundação Oswaldo Cruz, Rio de Janeiro. The reproductive system morphology was observed and drawn with the aid of the *camera lucida* attached to a Nikon stereomicroscope. Identification was made based on external morphology, color pattern, radula, jaw and reproductive system morphology through comparison with the original description of *Aphelodoris antillensis* and subsequent works (Bergh, 1879, 1980; Ev. Marcus and Er. Marcus, 1967; Hamann, 1992; Valdés *et al*., 2006).

SYSTEMATICS

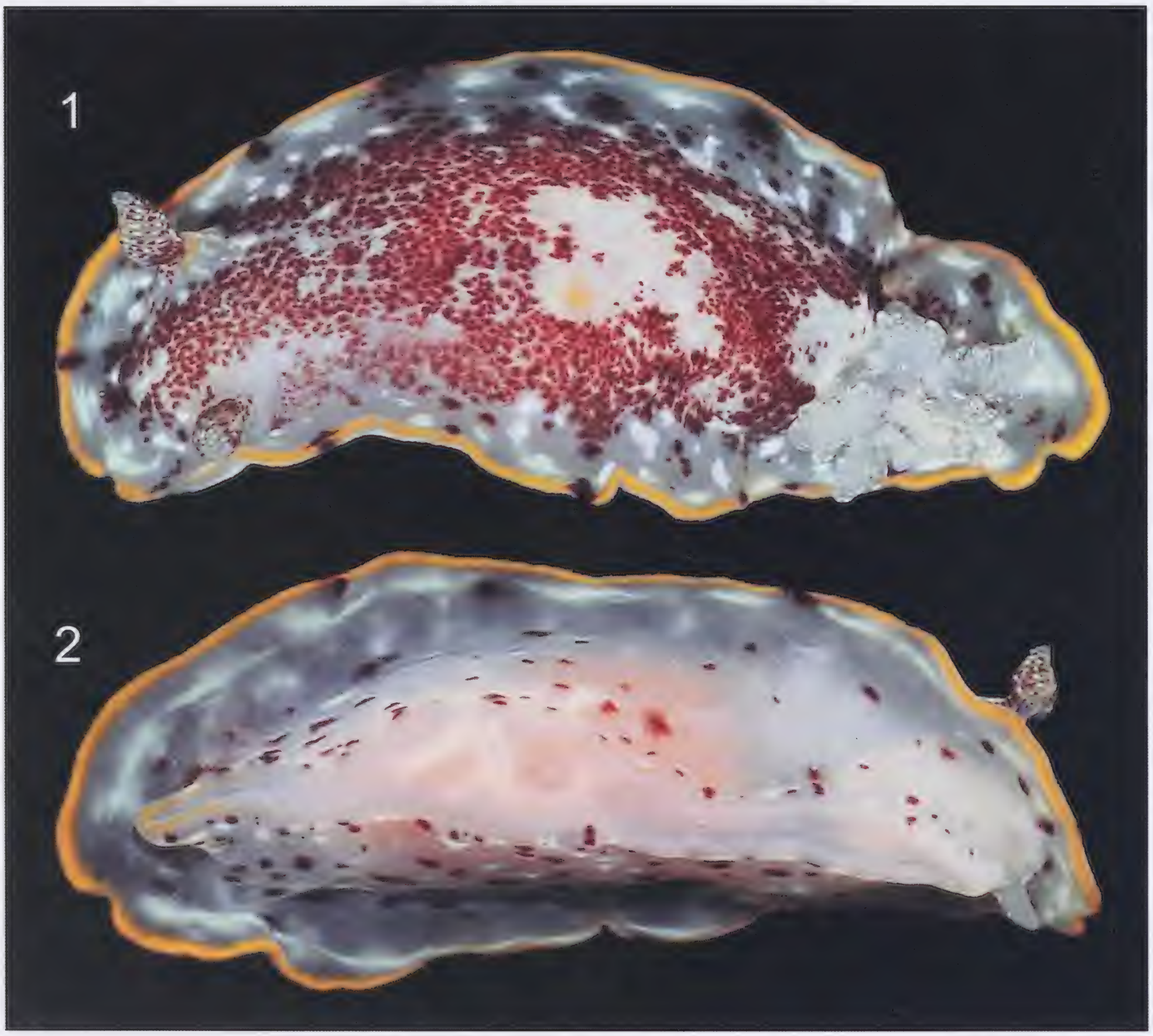
Order Nudibranchia Cuvier, 1817
Family Dorididae Rafinesque, 1815

Genus *Aphelodoris* Bergh, 1879

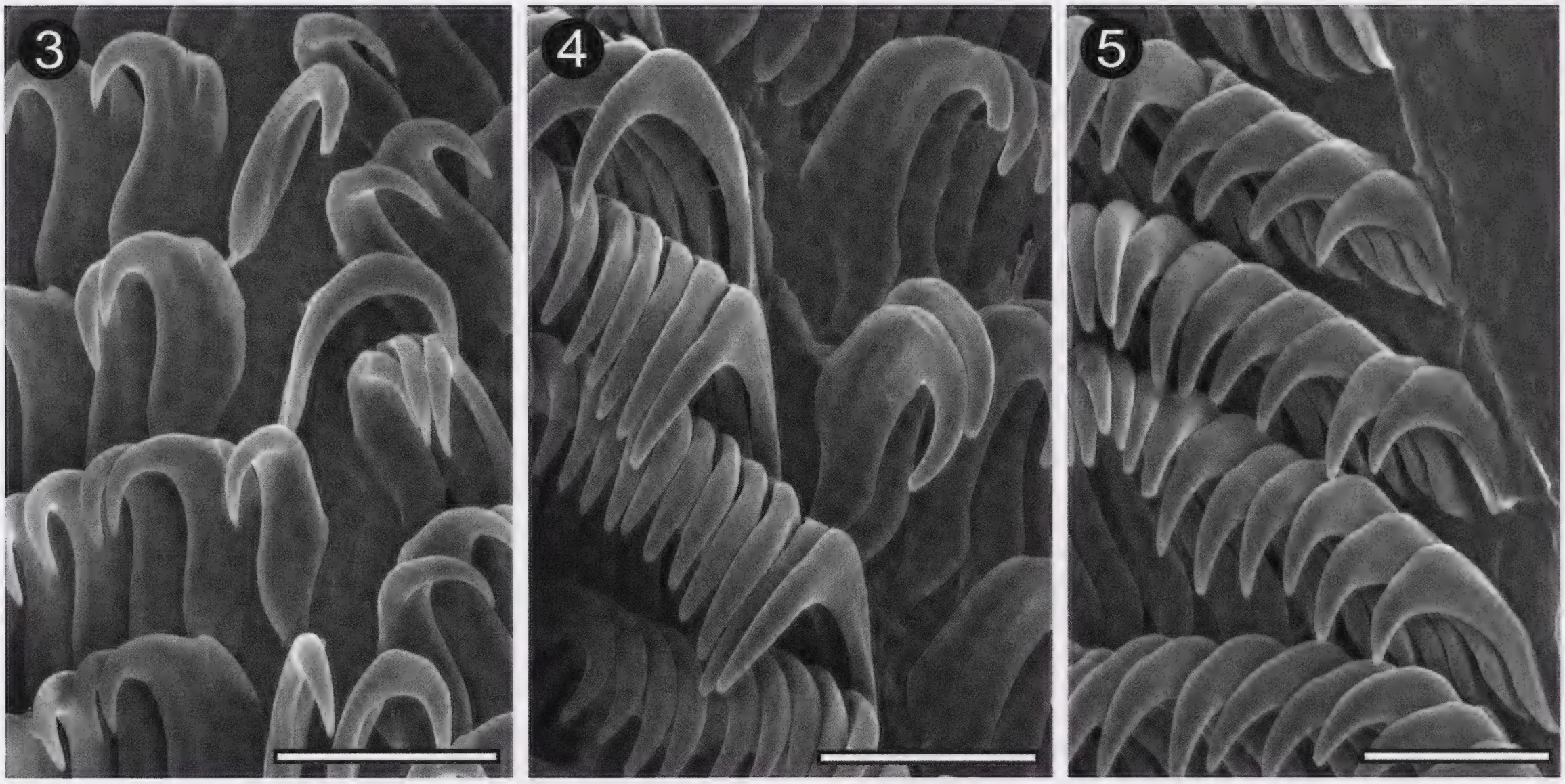
***Aphelodoris antillensis* Bergh, 1879**
(Figures 1–6)

Doris (?) *bistellata* Verrill, 1900: 548, pl. 66, Figure 2. Type locality: Castle Harbour, Bermuda.

External Morphology and Color (Figures 1–2): Living specimen 14 mm long. Dorsum smooth, without tubercles. Mantle translucent-white, mantle bordered by a yellow line. Dorsal mantle scattered by small irregular reddish-brown spots, absent on central dorsum; a small irregular yellow patch present on central dorsum. Submarginal mantle with irregular white spots. Rhinophores conical, with ten lamellae, translucent-white, speckled in reddish-brown. Rhinophoral sheath edge yellow.



Figures 1–2. *Aphelodoris antillensis,* external morphology, 14 mm long (MNRJ 58218). **1.** Dorsal view. **2.** Ventral view.



Figures 3–5. *Aphelodoris antillensis,* radula (MNRJ 58218). **3.** Innermost teeth. **4.** Lateral teeth. **5.** Marginal teeth. Scale bar: 40 µm.

Gill with five thick leaves, translucent-white with very small white and brown spots. Foot translucent-white with small brown spots of different sizes. Posterior end of the foot pigmented in yellow.

Radula (Figures 3–5): Radular formula 26 × 42.0.42. All teeth hook-shaped, unicuspid. Innermost teeth and lateral teeth with a large base and elongated cusp. Lateral teeth larger with blunted cusp. Marginal teeth smaller.

Reproductive System (Figure 6): Hermaphroditic ampulla long and curved; granular prostate connected to a short and muscular deferent duct; penial portion large, rounded. Seminal receptacle long, piriform; uterine duct large, conspicuous. Uterine duct connects to the bursa copulatrix very near to connection of the vagina. Bursa copulatrix large, rounded. Proximal portion of the vagina thin, becoming larger distally, near the gonopore. Female gland large, irregular in shape.

Material Examined: One specimen, 14 mm long alive, collected at Ilha da Âncora (22°46′10″ S, 41°47′20″ W), Armação dos Búzios, RJ, Brazil, 10 m depth, 9 February 2019, V. Padula coll. (MNRJ 58218).

Geographic Distribution: St. Thomas, Virgin Islands (type locality) (Bergh, 1879, 1880), Bermuda (Verrill, 1900; Hamann, 1992), Bahamas (Redfern, 2013), Florida (Ev. Marcus and Er. Marcus, 1967), Mexico, Costa Rica, Panama, Aruba, Curaçao, Cayman Islands, Jamaica, Dominican Republic, Puerto Rico, Virgin Islands, Antigua, St. Martin, Guadeloupe, Martinique, St. Lucia, St. Vincent & The Grenadines, Grenada south to Colombia and Venezuela (Hamann, 1992; Quiroga *et al.,* 2004; Valdés *et al.* 2006) and southeastern Brazil (present study).

DISCUSSION

The original description of *Aphelodoris antillensis* was based on the examination of two specimens from St. Thomas, Virgin Islands (Bergh, 1879: 108). Although lacking figures, the original description is very detailed and provides information about internal features, such as the smooth labial cuticle, absence of rachidian teeth, radular teeth hook-shaped, large prostate, and unarmed penis. Bergh (1879) also mentioned the presence of five thickened gill leaves. Figures of the original material examined by Bergh (1879) are provided in Bergh (1880, pl. 16) and are mostly of the radular teeth morphology. Ev. Marcus and Er. Marcus (1963) reported the species from Curaçao, by studying a 15 mm-long specimen collected in Piscadera Bay and Ev. Marcus and Er. Marcus (1967) further recorded the species from Puerto Rico and Florida. The reproductive system illustrated by Ev. Marcus and Er. Marcus (1967: 92) shows the diagnostic features of *A. antillensis*, such as the large granular prostate and the very close connection between the uterine duct and the vagina with the bursa copulatrix. The reproductive system of the specimen (Figure 6) matches that illustrated by Ev. Marcus and Er. Marcus (1967). This last work reported intraspecific variation in color in *A. antillensis* when comparing specimens from Curaçao, Florida and Puerto Rico. Subsequent works described the whitish mantle with different amount of dark red or brown pigments of *A. antillensis* while expanding the species range to Panama, Jamaica and Barbados (Meyer, 1977; Thompson, 1980; Edmunds and Just, 1985).

A larger study by Hamann (1992) based on specimens of *A. antillensis* from different localities across the

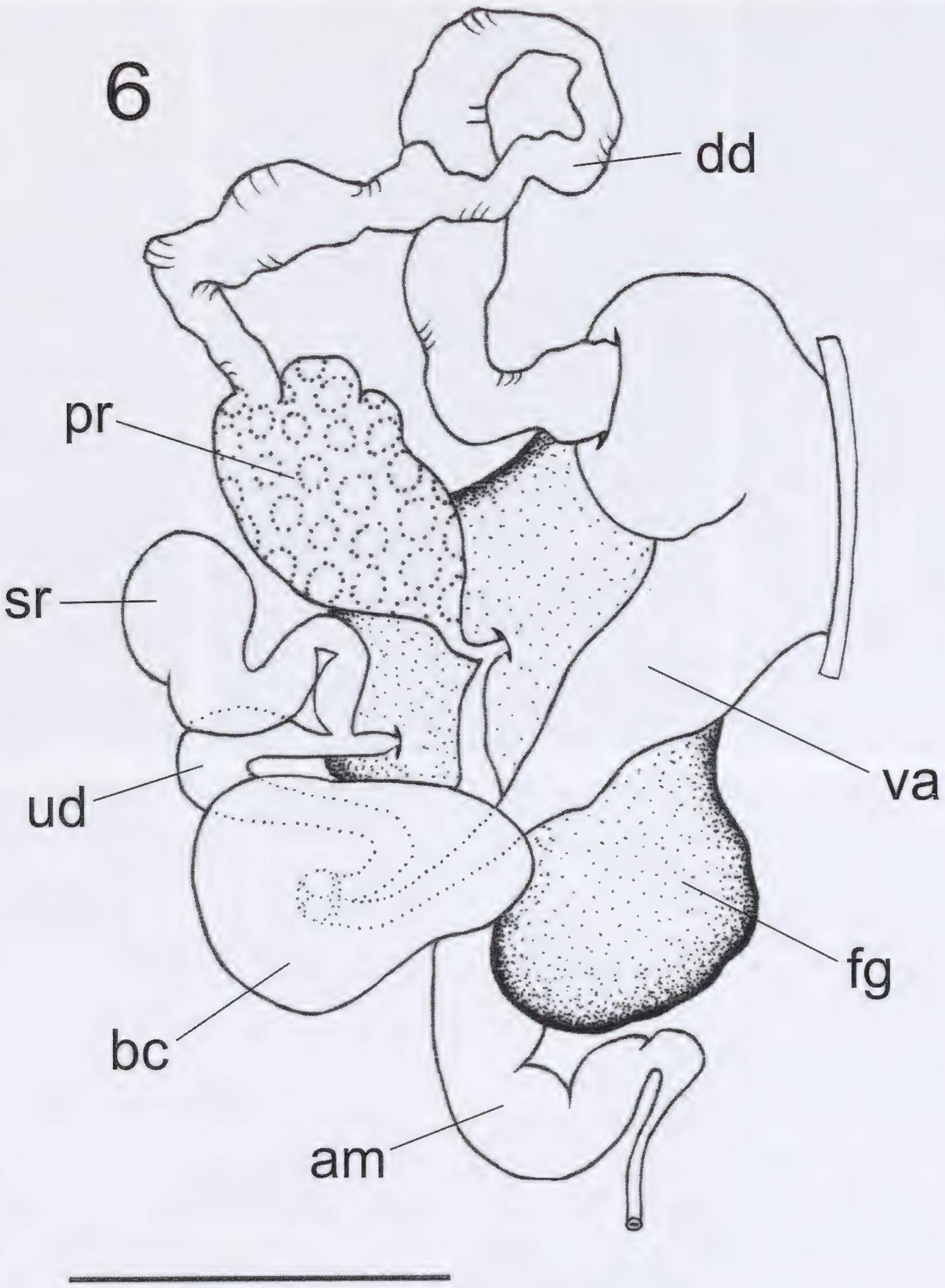


Figure 6. *Aphelodoris antillensis,* reproductive system (MNRJ 58218). Abbreviations: **am** = ampulla; **bc** = bursa copulatrix; **dd** = deferent duct; **fg** = female gland; **pr** = prostate; **sr** = seminal receptacle; **ud** = uterine duct; **va** = vagina. Scale bar: 1 mm.

Caribbean Sea explored the intraspecific variation in the body color pattern, the presence of a secondary cusp in the innermost radular teeth, as reported by Bergh (1979, 1980), and the presence of small tubercles on the mantle, described by Meyer (1977) and Thompson (1980). In his work, Hamman (1992) concluded that *Chromodoris bistellata* (Verrill, 1900) from Bermuda is, in fact, a junior synonym of *A. antillensis.* Hamman (1992) illustrated bright and dark color forms of *A. antillensis* and provided information about the radula and reproductive system of new specimens, characters that show less variation than color pattern and that are therefore more useful in the species identification. The specimen studied herein resembles the one from Venezuela illustrated by Hamman (1992, fig. 1F) in the amount of dark-red pigment and the presence of a marginal yellow line. As most specimens studied up to date, our material does not present a secondary cusp in the first lateral teeth and dorsal tubercles on the mantle. Exceptionally, Valdés (2002) reported 5–6 denticles on the inner side of the first lateral teeth of a specimen from Quintana Roo, Mexico.

The present record of *Aphelodoris antillensis* in the southwestern Atlantic, coast of Brazil, expands its known geographic distribution more than 6,000 kilometers southward. There are other species recorded from the Caribbean Sea and the Brazilian coast, and the similarities between the nudibranch faunas of these regions were reported in the past (Ev. Marcus, 1977; Padula and Santos, 2006; Valdés *et al.*, 2006; Padula *et al.*, 2012; among others). Research in the still less explored subtidal zone through scuba diving will undoubtedly reveal more species from Brazil. Future research including molecular

data of specimens across the wide geographic range of *A. antillensis* may provide further information on the evolution and genetic diversity of the species.

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LITERATURE CITED

Alvim, J. and A.D. Pimenta. 2013. Taxonomic review of the family Discodorididae (Mollusca: Gastropoda: Nudibranchia) from Brazil, with descriptions of two new species. Zootaxa 3745(2): 152–198. https://doi.org/10.11646/zootaxa.3745.2.2

Bergh, L.S.R. 1879. Neue Chromodoriden. Malakozoologische Blatter 1: 87–116, pl. IV.

Bergh, L.S.R. 1880. On the nudibranchiate gasteropod mollusca of the north Pacific Ocean, with special reference to those of Alaska. Part II. Proceedings of the Academy of Natural Sciences of Philadelphia 32: 40–127.

Cetra, N. and A. Roche. 2019. Una nueva especie del género *Trapania* (Nudibranchia: Goniodorididae) para el Mar Argentino. Acta Zoológica Lilloana 63(2): 1–10. https://doi.org/10.30550/j.azl/2019.63.2/1

Edmunds, M. and H. Just. 1985. Dorid, Dendronotid and Arminid nudibranchiate mollusca from Barbados. Journal of Molluscan Studies 51: 52–63. https://doi.org/10.1093/oxfordjournals.mollus.a065881

Galvão Filho, H.C., A.K. Araújo, F.V. Silva, V.M. Azevedo, C.A. Meirelles, and H. Matthews-Cascon. 2015. Sea slugs (Gastropoda: Heterobranchia) from a poorly known area in North-east Brazil: filling gaps in Atlantic distributions. Marine Biodiversity Records 8: 1–11. https://doi.org/10.1017/S1755267215000494

Hamann, J.C. 1992. A warm water Atlantic synonymy, *Aphelodoris antillensis* equals *Chromodoris bistellata* (Opisthobranchia: Gastropoda). The Veliger 35(3): 215–221.

Jörger, K.M., T. Stoschek, A.E. Migotto, G. Haszprunar, and T.P. Neusser. 2014. 3D-microanatomy of the mesopsammic *Pseudovermis salamandrops* Marcus, 1953 from Brazil (Nudibranchia, Gastropoda). Marine Biodiversity 44(3): 327–341. https://doi.org/10.1007/s12526-014-0224-5

Lima, P.O.V. and L.R.L. Simone. 2018. Revision of *Platydoris angustipes* and description of a new species of *Platydoris* (Gastropoda: Nudibranchia) from southeastern Brazil based on comparative morphology. Zoosystematics and Evolution 94(1): 1–15. https://doi.org/10.3897/zse.94.14959

Marcus, Ev. 1977. An annotated checklist of the western Atlantic warm water opisthobranchs. Journal of Molluscan Studies 4: 1–23. https://doi.org/10.1093/oxfordjournals.mollus.a065405

Marcus, Ev. and Er. Marcus. 1963. Opisthobranchs from the Lesser Antilles. Studies on the Fauna of Curaçao and other Caribbean Islands 19: 1–76.

Marcus, Ev. and Er. Marcus. 1967. American opisthobranch mollusks Part I, Tropical American opisthobranchs, Part II, Opisthobranchs from the Gulf of California. Studies in Tropical Oceanography 6(1–2): 1–256.

Marcus, Er. and Ev. Marcus. 1970. Opisthobranchs from Curacao and faunistically related regions. Studies on the fauna of Curaçao and other Caribbean Islands 122, 33: 1–129.

Meyer, K.B. 1977. Dorid nudibranchs of the Caribbean coast of the Panama Canal zone. Bulletin of Marine Science 27: 299–307.

MolluscaBase eds. 2022. MolluscaBase. *Aphelodoris* Bergh, 1879. Accessed through: World Register of Marine Species Available: https://www.marinespecies.org/aphia.php?p=taxdetails&id=415066 Accessed 2022-02-12.

Padula, V. and F.N. Santos. 2006. Three new records of Nudibranchia (Mollusca, Gastropoda) - additions on the Brazilian biodiversity. Biociências 14: 214–220.

Padula, V., J. Bahia, M.D. Correia, and H. Sovierzoski. 2012. New records of opisthobranchs (Mollusca: Gastropoda) from Alagoas, north-eastern Brazil. Marine Biodiversity Records 5: 1–11. https://doi.org/10.1017/S1755267212000346

Padula, V., A.K. Araújo, H. Matthews-Cascon, and M. Schrödl. 2014. Is the Mediterranean nudibranch *Cratena peregrina* (Gmelin, 1791) present in the Brazilian coast? Integrative species delimitation and description of *Cratena minor* n. sp. Journal of Molluscan Studies 80(5): 575–584. https://doi.org/10.1093/mollus/eyu052

Quiroga, S., N.E. Ardila, and M. Bolaños. 2004. *Aphelodoris antillensis* Berg, 1897 (Opisthobranchia: Nudibranchia: Doridídae), first record from the Colombian Caribbean. Boletín de Investigaciones Marinas y Costeras 33: 257–259.

Redfern, C. 2001. Bahamian Seashells: A thousand species from Abaco, Bahamas. Bahamianseashells.com, Inc. Boca Raton, Florida. 280 pp.

Thompson, T.E. 1980. Jamaican opisthobranch molluscs II. Journal of Molluscan Studies 46: 74–99. https://doi.org/10.1093/oxfordjournals.mollus.a065525

Valdés, A. 2002. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). Zoological Journal of the Linnean Society 136: 535–636. https://doi.org/10.1046/j.1096-3642.2002.00039.x

Valdés, A., J. Hamann, D.W. Behrens, and A. DuPont. Caribbean Sea Slugs. Sea Challengers Natural History Books, Gig Harbor. vii + 289 pp.

Verrill, A.E. 1900. The nudibranchs and naked tectibranchs of the Bermudas. Transactions of the Connecticut Academy of Arts and Sciences 10: 54–550, pl. 66.

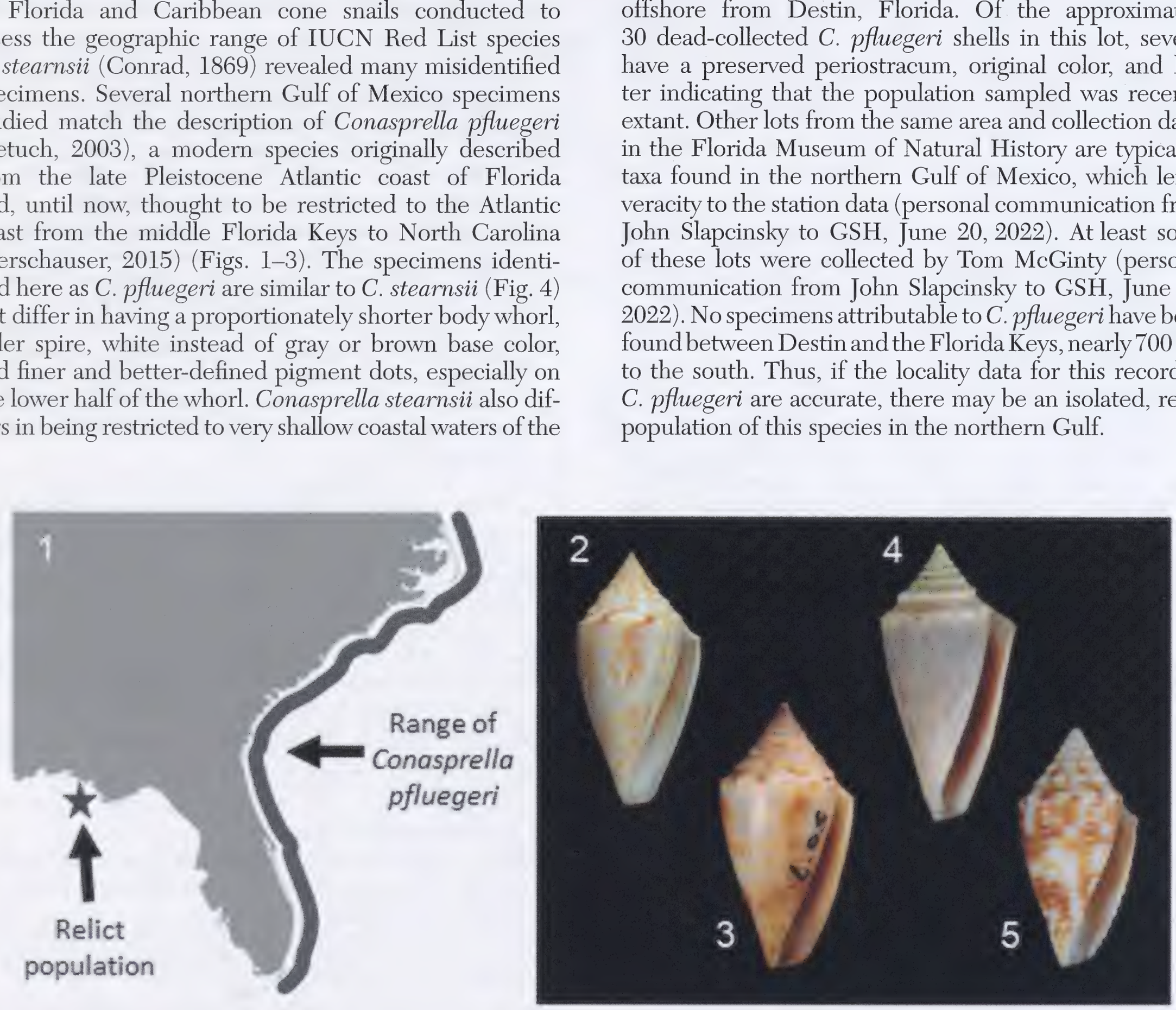
Wilson, N.G. 2003. Australian *Aphelodoris* (Mollusca: Nudibranchia): two new species, sperm ultrastructure and a redescription of *Aphelodoris greeni* Burn. In: F.E. Wells and D.I. Walker (eds), The Marine Flora and Fauna of Dampier, Western Australia. Western Australian Museum, Perth, 2: 563–587.

Research Note

Discovery of a relict population of the cone snail *Conasprella pfluegeri* (Gastropoda: Conidae) in the northeastern Gulf of Mexico

A survey of museum, university, and private collections of Florida and Caribbean cone snails conducted to assess the geographic range of IUCN Red List species *C. stearnsii* (Conrad, 1869) revealed many misidentified specimens. Several northern Gulf of Mexico specimens studied match the description of *Conasprella pfluegeri* (Petuch, 2003), a modern species originally described from the late Pleistocene Atlantic coast of Florida and, until now, thought to be restricted to the Atlantic coast from the middle Florida Keys to North Carolina (Berschauser, 2015) (Figs. 1–3). The specimens identified here as *C. pfluegeri* are similar to *C. stearnsii* (Fig. 4) but differ in having a proportionately shorter body whorl, taller spire, white instead of gray or brown base color, and finer and better-defined pigment dots, especially on the lower half of the whorl. *Conasprella stearnsii* also differs in being restricted to very shallow coastal waters of the eastern Gulf of Mexico (Avery et al., in prep.) in contrast to the offshore depths of these Gulf *C. pfluegeri* specimens. Another eastern Gulf species, *Conasprella pealii* (Green, 1830), has darker coloration and strong spiral ribs and lacks the pigment dots (Fig. 5).

The northern Gulf of Mexico specimens of *C. pfluegeri* (UF 191407) were collected between 1939 and 1941 in 25.6 m of water recorded as 9.6 km east and 6.4 km offshore from Destin, Florida. Of the approximately 30 dead-collected *C. pfluegeri* shells in this lot, several have a preserved periostracum, original color, and luster indicating that the population sampled was recently extant. Other lots from the same area and collection dates in the Florida Museum of Natural History are typical of taxa found in the northern Gulf of Mexico, which lends veracity to the station data (personal communication from John Slapcinsky to GSH, June 20, 2022). At least some of these lots were collected by Tom McGinty (personal communication from John Slapcinsky to GSH, June 20, 2022). No specimens attributable to *C. pfluegeri* have been found between Destin and the Florida Keys, nearly 700 km to the south. Thus, if the locality data for this record of *C. pfluegeri* are accurate, there may be an isolated, relict population of this species in the northern Gulf.



Figures 1–5. *Conasprella pfluegeri*. Range and morphologically related species. **1.** Map of the range of ***Conasprella pfluegeri***, including relict population off Destin, Florida in the Gulf of Mexico. **2.** Holotype of ***Conasprella pfluegeri*** from the Pleistocene Fort Thompson Fm., Belle Glade, Palm Beach Co., Florida, AMNH 308069, 25 mm. **3. *Conasprella pfluegeri*** from 25.6 m of water, 9.6 km east and 6.4 km offshore from Destin, Okaloosa Co., Florida, UF 191407, 15 mm. **4. *Conasprella stearnsii*** from the west end of Clam Factory Shoal, Caxambas Bay, Collier Co., Florida, in sand, Marlo Krisberg coll., 21 mm. **5. *Conasprella pealii*** from Sanibel Beach, Lee Co., Florida, BMSM 26598, 15 mm.

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Gulf relict populations of predominantly Atlantic species have been documented in other marine taxa, such as the bivalve *Donax variabilis* Say, 1822 (Adamkewicz and Harasewych, 1996), the gastropod *Stramonita floridana* (Conrad, 1837) (Claremont et al., 2011), the hermit crab *Pagurus* Fabricius, 1775 (Cunningham et al., 1991), and the stone crab *Menippe* De Hann, 1833 (Bert, 1986). Petuch and Berschauer (2020) have elevated populations of some of these isolated Gulf populations to subspecies status. Many authors have speculated that northern Gulf-Atlantic connections were the result of an ancient seaway, the Suwannee Strait, that once crossed the northern part of the Florida peninsula (Bert, 1986; Webb, 1990; Cunningham et al., 1991; Felder and Staton, 1994; Randazzo and Jones, 1997; Lee and Foighil, 2005). However, the Suwannee Strait closed by the late Oligocene or early Miocene, roughly 25 million years ago (Popenoe et al., 1987; Gardulski et al., 1991), whereas population connections across the peninsula estimated from genetic distances are more recent, e.g., within the last 1 million years (Bert, 1986). A simpler explanation is provided by Pleistocene climate cycles. Today, the peninsula of Florida extends into subtropical waters, creating a biogeographic transition between temperate and tropical faunas around Cape Canaveral on the Atlantic coast and Naples on the Gulf side (Briggs, 1974). During periods of glacial cooling, this transition zone shifts southward, allowing temperate populations on either side to expand around the Florida peninsula (Avise, 1992). During subsequent warming periods, this transition shifts back northward, isolating Gulf and Atlantic populations.

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LITERATURE CITED

Adamkewicz, S.L. and M.G. Harasewych. 1996. Systematics and biogeography of the genus *Donax* (Bivalvia: Donacidae) in eastern North America. American Malacological Bulletin 13: 97–103.

Avise, J.C. 1992. Molecular population structure and the biogeographic history of a regional fauna: a case history with lessons for conservation biology. Oikos 63: 62–76.

Berschauer, D.P. 2015. A comparison of adaptive radiation in Conidae and Conilithidae (Gastropoda: Conoidea) in the Eastern and Western Atlantic, together with an iconography of the conilithid genus *Jaspidiconus*. The Festivus 47: 99–113.

Bert, T.M. 1986. Speciation in western Atlantic stone crabs (genus *Menippe*): the role of geological processes and climatic events in the formation and distribution of species. Marine Biology 93: 157–170.

Claremont, M., S.T. Williams, T.G. Barraclough, and D.G. Reid. 2011. The geographic scale of speciation in a marine snail with high dispersal potential. Journal of Biogeography 38: 1016–1032.

Cunningham, C.W., L.W. Buss, and C. Anderson. 1991. Molecular and geologic evidence of shared history between hermit crabs and the symbiotic genus *Hydractinia*. Evolution 45: 1301–1316.

Gardulski, A.F., M.H. Gowen, A. Milsark, S.D. Weiterman, S.W. Wise Jr., and H.T. Mullins. 1991. Evolution of a deep-water carbonate platform: Upper Cretaceous to Pleistocene sedimentary environments on the west Florida margin. Marine Geology 101: 163–179.

Lee, T. and D. Foighil. 2005. Placing the Floridian marine genetic disjunction into a regional evolutionary context using the scorched mussel, *Brachidontes exustus*, species complex. Evolution 59: 2139–2158.

Petuch, E.J. and D.P. Berschauer. 2020. Tropical Marine Mollusks: An Illustrated Biogeographical Guide. CRC Press, London, New York, Boca Raton, 357 pp.

Popenoe, P., V.J. Henry, and F.M. Idris. 1987. Gulf trough—the Atlantic connection. Geology 15: 327–332.

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Research Note

A new name for *Valdesia* del Río, 1985 (Cenozoic fossil Mollusca), junior homonym of *Valdesia* Maury, 1981 (extant Arachnida)

Valdesia del Río, 1985 (type species *Valdesia valdesiensis* del Río, 1985, by original designation) was originally introduced to include three late Miocene fossil gastropod species from Argentina (Puerto Madryn Formation), then thought to correspond to Architectonicidae but later shown to belong in Trochidae (Martínez et al., 1998). However, there exists a senior homonym, *Valdesia* Maury, 1981 (type species *Valdesia simplex* Maury, 1981, by original designation), a genus of extant camel spiders (Solifugae) of the family Daesiidae. Both were named after Valdés Peninsula in Chubut, Argentina.

The new name ***Molvaldesia* del Río nomen novum**, alluding to its original name and placement in Mollusca, is here proposed to replace *Valdesia* del Río, 1985 in accordance with ICZN articles 56.1, 60.1, and 60.3 (ICZN, 1999).

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LITERATURE CITED

del Río, C. J. 1985. Primera mención de la subfamilia Architectonicinae (Mollusca: Gastropoda) en el Terciario de la Patagonia (República Argentina). Ameghiniana 22(3-4): 263–268.

ICZN 1999. International Code of Zoological Nomenclature, 4th edition. The International Trust for Zoological Nomenclature.

Martínez Chiapara, S.A., C.J. del Río, and V. Reichler. 1998. Clase Gastropoda. In: C.J. del Río (Ed.) Moluscos marinos Miocenos de la Argentina y del Uruguay. Monografías de la Academia Nacional de Ciencias Exactas, Físicas y Naturales (Buenos Aires) 15: 26-47.

Maury, E.A. 1981. Un nuevo género de Daesiidae de la Argentina (Arachnida: Solifugae). Comunicaciones del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia". Entomología 1(5): 75–82.

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Notice

The Mayer-Eymar collection of Cenozoic mollusks

Karl Mayer-Eymar (1826–1906) was a Swiss stratigrapher and paleontologist who worked at the geological department of the Federal Institute of Technology ("Eidgenössische Technische Hochschule," ETH) in Zurich. He is the author of more than 175 publications, mostly on Cenozoic mollusks, in which he described more than 1,100 new bivalve and gastropod species. In addition, he erected 13 new Cenozoic stages, five of them still in use today. Both stages and new taxa were based on his huge collection of more than 500,000 fossil specimens. The Mayer-Eymar collection of Cenozoic mollusks is therefore of paramount importance to both mollusk taxonomists and stratigraphers.

About fifty years ago, a short notice by Peter Jung of the Natural History Museum Basel appeared in this journal (Jung, 1972), announcing that the Mayer-Eymar collection had been transferred in 1966 from the ETH to the Basel Museum and was since then administered and curated there. It remained for more than 50 years at the Basel Museum. With this new notice I want to inform the interested paleontologists that the collection was transferred in late 2020 back to the ETH in Zurich, where it is now accessible.

LITERATURE CITED

Jung, P. 1972. The Collection of Karl Mayer-Eymar. The Nautilus 85(4): iii.

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